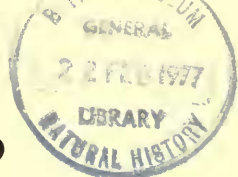


# EVOLUTION OF THE SILURIAN AND DEVONIAN GRAPTOLIDS



BY

RICHARD BARRIE RICKARDS

Sedgwick Museum, Cambridge

JANA ELIZABETH HUTT

Milltimber, Aberdeen

AND

WILLIAM BENJAMIN NEWELL BERRY

Department of Paleontology, University of California

*Pp 1-120 ; 6 Plates ; 55 Text-figures*

BULLETIN OF  
THE BRITISH MUSEUM (NATURAL HISTORY)  
GEOLOGY

Vol. 28 No. 1

LONDON: 1977

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), instituted in 1949, is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 a separate supplementary series of longer papers was instituted, numbered serially for each Department.

This paper is Vol. 28, No. 1 of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.

World List abbreviation  
*Bull. Br. Mus. nat. Hist. (Geol.)*

ISSN 0007-1471

© Trustees of the British Museum (Natural History), 1977

BRITISH MUSEUM (NATURAL HISTORY)

Issued 24 February, 1977

Price £11.90



# EVOLUTION OF THE SILURIAN AND DEVONIAN GRAPTOLOIDS

By R. B. RICKARDS, J. E. HUTT & W. B. N. BERRY

## CONTENTS

	<i>Page</i>
ABSTRACT . . . . .	5
I. INTRODUCTION . . . . .	5
II. GENERAL EVOLUTIONARY FRAMEWORK . . . . .	9
III. ORDOVICIAN REMNANTS . . . . .	11
1. ' <i>Amplexograptus</i> ' and the <i>Climacograptus innotatus</i> group . . . . .	11
2. <i>Pseudoclimacograptus</i> . . . . .	14
3. <i>Diplograptus</i> . . . . .	16
4. <i>Climacograptus</i> . . . . .	16
IV. SILURIAN BISERIAL GRAPTOLOIDS AND DERIVATIVES . . . . .	19
A. Groups with periderm entire . . . . .	19
5. <i>Akidograptus ascensus</i> . . . . .	19
6. <i>Glyptograptus</i> . . . . .	20
7. <i>Glyptograptus</i> ( <i>Pseudoglyptograptus</i> ) . . . . .	21
8. <i>Dimorphograptus</i> (' <i>Dimorphograptus</i> ') . . . . .	23
9. <i>Rhaphidograptus</i> . . . . .	24
10. <i>Cystograptus</i> . . . . .	25
11. <i>Orthograptus</i> . . . . .	25
12. <i>Orthograptus acuminatus</i> . . . . .	28
13. <i>Dimorphograptus</i> (' <i>Bulmanograptus</i> ') . . . . .	28
14. <i>Petalograptus</i> . . . . .	28
15. <i>Cephalograptus</i> . . . . .	30
B. The Retiolitids . . . . .	30
16. <i>Retiolites</i> , <i>Stomatograptus</i> and <i>Sinostomatograptus</i> . . . . .	31
17. <i>Pseudoretiolites</i> and <i>Pseudoplegmatoraptus</i> . . . . .	33
18. <i>Plectograptus</i> ?, <i>Plectograptus</i> and <i>Paraplectograptus</i> . . . . .	34
19. <i>Gothograptus</i> , <i>Holoretiolites</i> and <i>Spinograptus</i> . . . . .	34
V. MONOGRAPTINID EVOLUTION . . . . .	36
20. The Origin of Monograptids . . . . .	36
21. The <i>atavus</i> group ( <i>Atavograptus</i> ) and <i>A. strachani</i> . . . . .	39
22. <i>Pribylograptus</i> . . . . .	40
23. <i>Coronograptus</i> . . . . .	41
24. <i>Lagarograptus</i> . . . . .	42
25. The ' <i>revolutus</i> ' group with simple hooks . . . . .	42
26. The ' <i>revolutus</i> ' group with thecal horns . . . . .	44
27. The <i>sudburiae</i> group, a new group of biform monograptids . . . . .	45
28. ' <i>Demirastrites</i> ' . . . . .	46
29. <i>Rastrites</i> . . . . .	47
30. <i>Monograptus sedgwickii</i> . . . . .	48
31. ' <i>Pernerograptus</i> ' . . . . .	51
32. ' <i>Campograptus</i> ' . . . . .	52
33. <i>Monoclimacis</i> . . . . .	54
34. <i>Monograptus</i> s.s. (including <i>Mediograptus</i> ) . . . . .	56
35. <i>Pristiograptus</i> . . . . .	62

	<i>Page</i>
36. ' <i>Streptograptus</i> ' . . . . .	67
37. <i>Diversograptus</i> , <i>Sinodiversograptus</i> and <i>Barrandeograptus</i> .	71
38. ' <i>Spirograptus</i> ' . . . . .	72
39. <i>Oktavites</i> . . . . .	73
40. <i>Averianowograptus</i> and <i>Uralograptus</i> . . . . .	74
41. <i>Cyrtograptus</i> . . . . .	76
42. <i>Saetograptus</i> and <i>M. ludensis</i> . . . . .	77
43. <i>M. bugensius</i> and <i>M. hercynicus</i> . . . . .	78
44. <i>Bohemograptus</i> . . . . .	82
45. <i>Neocucullograptus</i> and <i>Neolobograptus</i> . . . . .	82
46. <i>Neodiversograptus</i> . . . . .	82
47. <i>Cucullograptus</i> and <i>Lobograptus</i> . . . . .	82
48. <i>Linograptus</i> and <i>Abeisograptus</i> . . . . .	82
VI. SUMMARY OF SILURIAN TRENDS . . . . .	83
Variable rhabdosome curvature . . . . .	86
Dorsally curved and spiral rhabdosomes . . . . .	86
Ventrally curved rhabdosomes . . . . .	88
Proximal protraction . . . . .	88
Thecal elongation . . . . .	88
Thecal introversion . . . . .	89
Ventral thecal processes . . . . .	90
Retroversion . . . . .	90
Thecal hooks . . . . .	90
Thecal isolation . . . . .	91
Thecal triangulation . . . . .	92
Gracile and robust rhabdosomes . . . . .	92
Prothecal folds . . . . .	94
Thecal and sicular spinosity . . . . .	94
Sicular cladia . . . . .	95
Thecal cladia . . . . .	95
Thecal asymmetry . . . . .	96
VII. SYSTEMATIC SECTION . . . . .	96
Genus <i>Climacograptus</i> Hall . . . . .	97
<i>Climacograptus innotatus pacificus</i> Ruedemann . . . . .	97
<i>Climacograptus typicalis</i> Hall . . . . .	97
<i>Climacograptus nebula</i> (Toghill & Strachan) . . . . .	98
Genus <i>Pseudoclimacograptus</i> Přibyl . . . . .	98
Subgenus <i>Pseudoclimacograptus</i> Přibyl . . . . .	98
<i>Pseudoclimacograptus (P.) orientalis</i> Obut & Sobolevskaya .	98
Subgenus <i>Metaclimacograptus</i> Bulman & Rickards . . . . .	98
<i>Pseudoclimacograptus (Metaclimacograptus) sp.</i> . . . . .	98
Genus <i>Akidograptus</i> Davies . . . . .	98
<i>Akidograptus ascensus</i> Davies . . . . .	98
Genus <i>Glyptograptus</i> Lapworth . . . . .	99
Subgenus <i>Glyptograptus</i> Lapworth . . . . .	99
<i>Glyptograptus (G.) persculptus</i> (Salter) . . . . .	99
<i>Glyptograptus (G.) serratus barbatus</i> Elles & Wood . . . . .	99
' <i>Comograptus</i> ' <i>comatus</i> Obut & Sobolevskaya . . . . .	100
Genus <i>Orthograptus</i> Lapworth . . . . .	100
<i>Orthograptus mutabilis</i> Elles & Wood . . . . .	100
<i>Orthograptus insectiformis</i> (Nicholson) . . . . .	101
<i>Orthograptus bellulus</i> Törnquist . . . . .	101
<i>Orthograptus cyperoides</i> Törnquist . . . . .	101

	<i>Page</i>
Genus <i>Rhaphidograptus</i> Bulman . . . . .	102
<i>Rhaphidograptus toernquisti</i> (Elles & Wood) . . . . .	102
Genus <i>Dimorphograptus</i> Lapworth . . . . .	102
<i>Dimorphograptus</i> sp. . . . .	102
Genus <i>Atavograptus</i> Rickards . . . . .	102
<i>Atavograptus praestrachani</i> sp. nov. . . . .	102
Genus <i>Pribylograptus</i> Obut & Sobolevskaya . . . . .	103
Genus <i>Coronograptus</i> Obut & Sobolevskaya . . . . .	103
Genus <i>Lagarograptus</i> Obut & Sobolevskaya . . . . .	103
Genus <i>Monograptus</i> Geinitz . . . . .	104
<i>Monograptus sudburiae</i> Hutt . . . . .	104
<i>Monograptus delicatulus</i> Elles & Wood . . . . .	104
<i>Monograptus walherae</i> nom. nov. . . . .	104
<i>Monograptus</i> sp. A . . . . .	105
<i>Monograptus turriculatus</i> Barrande . . . . .	105
Genus <i>Pristiograptus</i> Jaekel . . . . .	105
<i>Pristiograptus</i> spp. 1 and 2 . . . . .	105
VIII. IN RETROSPECT . . . . .	106
IX. REFERENCES . . . . .	109
X. INDEX . . . . .	114

## ABSTRACT

The evolution of the whole of the Silurian and Devonian graptoloids, that is about one-quarter of known graptolites, is discussed. For the most part actual specific lineages are described, whilst in section II *major* evolutionary concepts are only outlined on the broad evolutionary framework. A synopsis of Silurian 'trends' is given in section VI, and the extensive systematic notes (section VII) are a necessary result of the authors' investigations of the numerous groups and genera: no new taxa are proposed at the higher classificatory levels, but at generic and specific level considerable redefinition (e.g. *Atavograptus* Rickards, *Lagarograptus* Obut & Sobolevskaya) and description of newly recorded structures are required. *Atavograptus praestrachani* sp. nov. is described, and *Monograptus walherae* nom. nov. is proposed for *M. toernquisti* Sudbury non Eisel.

We interpret that all monograptid evolution stems from the *atavus* group (*Atavograptus*), and almost the whole of the post-Wenlock evolution from a pristiograptid stock. Each of these evolutionary explosions follows a period of near-extinction of the graptoloids. The origins of *Pristiograptus*, *Monoclimacis* and *Monograptus* (restricted) are considered to be firmly established herein, but a lack of recent research on some groups ('*Spirograptus*', '*Globosograptus*') defines some of the problem areas. A probable polyphyletic origin of a number of groups is proposed (*Monograptus*, *Retiolites*, *Climacograptus*). Some of the detailed morphological information accumulated, together with stratigraphical occurrences, has implication concerning the mode of life of the graptoloids, but this latter topic is considered beyond the scope of the present work and is largely ignored.

## I. INTRODUCTION

NOT SINCE Elles' (1922) work on the graptolite faunas of the British Isles has a comprehensive study been made of the evolution of the Silurian graptoloids. Elles devoted a good deal of her effort in that paper to the Ordovician graptoloids, but the accumulation of data on the Silurian graptoloids during the past fifty years, and in particular during the last decade, today precludes such an all-embracing

study. The actual lineages which Elles proposed as a framework to the plexus of Silurian graptoloids are summarized in the last table of her paper (1922:200). The present paper supports only about one-third of these lineages (e.g. the *crenularis-vomerina* line) which were erected mostly upon an understanding of the silhouettes of the graptoloid species. Those suggested lineages which most modern workers would readily support (e.g. the *triangulatus-longispinus* line, redefined by Sudbury, 1958) were those which Elles erected after study of pyritized three-dimensional specimens, the next best form of preservation to isolated or transparent material. In fact the main changes in the present understanding of the evolutionary lineages result as much from the access the writers have had to isolated and good three-dimensional material, as from the more refined stratigraphical studies of the last few years. Papers relevant to the last category include Rickards (1965, 1967, 1969, 1970), Burgess *et al.* (1970), Toghil (1968a, b), Teller (1964, 1969), Warren (1971), Koren' (1973), and Hutt & Rickards (1970).

Apart from this broadly based work of Elles there were important papers by Bulman (1958, 1963) similarly wide in scope, but not dealing with actual lineages, and in addition a number of papers on the detailed evolution of particular groups (Sudbury 1958, Urbanek 1966, 1970 etc.): these are discussed at appropriate points in the text below, both in section II on the broad evolutionary framework and in sections III-V on the detailed evolution.

The work on which the present paper is based started about 1966 independently in Berkeley, California, where one of us (W. B. N. B.) began constructing an evolutionary lineage diagram embracing Silurian and Devonian graptoloids, and at the British Museum (Natural History) where R. B. R. developed a similar diagram, based upon geological range and species abundance, during the research training of Miss J. E. Hutt. These diagrams, essentially sketchy at first, became refined as work on the various lineages progressed, and are included here as Fig. 1. It provides a basis for discussion or investigation of the evolution of any of the groups or genera. The construction of Fig. 1 is outlined below.

A. *Range in time of a group or genus.* In one sense the diagram could only be constructed after research had decided on the composition of a group: in practice the diagram has itself evolved since it has provided ideas. The stratigraphical occurrence of each of the species in a group or genus (represented by the 'balloons') is plotted against the zonal scheme to the left of the chart. Thus *Lagarograptus* is considered to range from the *acinaces* to *sedgwickii* Zones inclusive. The zonal scheme used is largely that adopted by Cocks *et al.* (1971) for pre-Pridoli strata, and also that used in Czechoslovakia (Bouček, personal communication) and Poland (Teller 1969) for post-Ludlow strata. Occasionally, where greater precision is not possible, reference of a species may be to a grosser zone such as the *gregarius* Zone *sensu* Elles & Wood (1901-18). The range in time of graptoloid species is considered on a *world-wide basis* and the writers have used all the means at their disposal to obtain a thoroughly international coverage of the literature and actual collections. Consequently some of the generic ranges may appear to be longer than one would expect from a perusal of the British literature only, but such information





is vital to an evolutionary understanding of the Graptoloidea. Naturally a considerable number of decisions have had to be made by the writers on the actual horizon of a species in terms of the 'standard' zonal scheme used, but it is their opinion that these decisions are themselves of great value. A drawback of such a composite chart is that some of the 'balloons' might be shown as more elongated than they should be, but where there is real doubt in the writers' minds, about either the horizon or generic assignation, they have tried to indicate this by judicious use of question marks and dashed lines.

B. *Species abundance*. The horizontal axis of the chart records the number of species recognized by the writers at any one zonal level. Thus *Lagarograptus* is represented by only one species at each zonal level or, where the lines are dashed, by lack of a record. Only in a few cases of dubious groupings ('*Spirograptus*' and '*Globosograptus*') are the 'balloons' smoothed out and approximate. In many cases the actual justification for the width of a 'balloon' is discussed in the appropriate section. For example, the *Diplograptus* occurrence is dealt with species by species in section III.3 (p. 16).

C. *Lineages*. A few lineages and 'key' species are located on the chart, particularly those forms mentioned by Elles (1922: 200) in the same context so that a direct comparison is possible. The main text of sections III-V deals in detail with these lineages.

Therefore, in spite of the obvious drawbacks to such a diagram (its subjectivity at various levels), the writers have found it a useful basis for discussion. It is immediately obvious that *Holoretiolites*, for example, cannot on present evidence give rise to the first gothograptids, and that dimorphograptids cannot give rise to the first monograptids: other tempting morphological derivations are similarly unavailable.

Sections III-V, then, expand the framework provided by Fig. 1. It should be emphasized that these sections are not merely reviews of previous work, but include a great deal of new information based upon our own investigations. This is particularly the case in the Llandovery and Wenlock Series, but applies also to a degree to post-Wenlock evolution. The work of Sudbury (1958) and of Urbanek (1966, 1970 etc.) is treated in relation to the whole and is, naturally, synoptic. However, throughout the rest of the text, the diagrams are original and the source of the information is quoted in those few instances where it is necessary.

By examining the evolution of the whole of the Graptoloidea it is possible to define certain areas in need of considerable revision or original work, and these are indicated at the appropriate points in the text in sections III-V. The writers have made a considerable effort to see the actual material upon which the evolutionary story depends. For example W. B. N. B. and R. B. R. were fortunate to be able to study Urbanek's (1966, 1970) collections at a time when that author was actively working on them, and, with the assistance of Professor Obut and Dr Koren', to examine almost all the Russian collections monographed, including the early studies of Averianow (1929) and Levina (1928).

A very brief review of this work has appeared in section 7 of the Montreal Congress (Hutt, Berry & Rickards 1972) whilst talks on various aspects of it, usually

accompanied by abstracts, have been given at the Palaeontological Association (Rickards & Hutt 1970), at the Geological Society of America (Berry 1969) and again at the Montreal Congress (Hutt *et al.* 1972, Abstracts : 226-7). The present authorship is of interest only in one further respect : in the early stages of the work there was a good deal of testy debate about who was responsible for which discovery, and it was decided that rather than spend the next decade or two in controversy the writers would join forces. The present manuscript was prepared in total by one of us (R. B. R.) and then assessed and criticized by the other two.

**TEXT-FIGURES.** The 'standard' zonal scheme used for the purposes of this paper is shown on the left of Fig. 1, while slightly more elaborated versions of the upper part, based largely on Polish research, are used in some diagrams such as Fig. 31. On each evolutionary diagram the known range of the species in time is indicated, in most cases by means of elongate rectangles : where the incoming and last occurrences of the species are somewhat doubtful the rectangle is broken into shorter fragments, and where there is real doubt about the occurrence we have put question marks in the appropriate positions.

The arrows shown connecting these ranges indicate the direction in which we think evolution took place : again we have placed question marks in areas of doubt. Illustrations of the species are usually given against the range rectangle, but to avoid any confusion the illustration is linked to the range either by means of an a-a notation or by fine tie lines : in several diagrams neither is necessary.

In general the illustrations are drawn from actual specimens, but where drawn from previous illustrations they have almost always been redrawn. In a few instances some idealized drawings have been included (e.g. Fig. 17).

We have attempted throughout to give magnifications and to keep all the magnifications on one figure the same, but sometimes, such as on the chart of the evolution of the cyrtograptids (Fig. 42), this has proved impracticable. However, magnifications are given in the figure explanations, as are the specimen numbers and depositories of the specimens, so that the illustrations can be checked directly.

**ACKNOWLEDGEMENTS.** We should like to thank collectively many colleagues throughout the world who have helped with loan of specimens and with information, often unpublished, relating to stratigraphy. Specimen depositories are indicated as follows : BM(NH), British Museum (Natural History), London ; SM, Sedgwick Museum, Cambridge ; LO, Lund University ; LU, Leicester University ; GSM, Geological Survey Museum (Institute of Geological Sciences) ; BU, Birmingham University ; HUR, Hull University Department of Geology, Rickards Collection ; AMNH, American Museum of Natural History ; USNM, United States National Museum ; TCD, Trinity College, Dublin.

## II. GENERAL EVOLUTIONARY FRAMEWORK

George (1962 : 41) considered thecal elaboration in graptolites a cladogenetic divergence, implying that major rhabdosomal changes involved anagenesis. In discussing the graptoloids Bulman (1963 : 407) took a similar view and defined the



following anagenetic grades in more or less ascending stratigraphic order: 1, multiramous; 2, tetragraptid; 3, didymograptid; 4, diplograptid; 5, monograptid. Cladogenetic divergence was exemplified in this last work by leptograptid and dicellograptid production from grade 3, by retiolitid, lasiograptid and glossograptid production from grade 4 and by 'dimorphograptid' production from grade 5. In stratigraphic terms grade 4 survives into the Silurian and grade 5 is typically Silurian. The present writers, therefore, in discussing the evolution of Silurian graptoloids, are dealing broadly with cladogenetic divergence, but also with the anagenetic change in grade from diplograptid to monograptid (sections 4, 5, 6, 8, 9, 11, 12 and 13 below).

Bulman (1963: 401) remained cautious, however, in applying Huxley's (1958) grades and ensuing cladogenesis to colonial organisms, pointing out (p. 402) that '... in any non-colonial group of organisms thecal characters would necessarily represent the natural and only basis for classification'. Changes in *rhabdosomal* form are almost always abrupt and discontinuous, for example an increase in length of the uniserial portion of the dimorphograptid stipe is extremely rare if not doubtful (Rickards 1963, 1970). George (1962: 41) considered thecal elaboration '... scarcely to be regarded as a "trend" (if the word is to contain as an element of its meaning a hint of channelled direction of limited variability); and most of the lineages are broadly monophyletic especially in the prolific diversity of early Silurian faunas'. We feel that the evidence of lineages and thecal elaboration described below tends to contradict this opinion, and would urge caution in applying the cladogenesis/anagenesis concept too rigidly.

For the most part, however, we outline below actual lineages of species, or suggested lineages and suggested problem areas, and avoid for the present major evolutionary concepts. Examination of Fig. 1, the construction of which was explained above (p. 6), shows that the Silurian and Devonian graptoloids enjoy two genuine evolutionary 'bursts' and suffered two crippling evolutionary 'lows' before extinction probably in the Emsian. Reasons for these 'lows' and 'bursts' are not discussed here, since at best our ideas are speculative, but it may be noted that both evolutionary expansions coincide with marked transgressions in the northern hemisphere, whilst the Ashgill 'low' is coeval with the strange Hirnantia fauna which is possibly a cold water fauna developed during glaciation in Africa and South America (Berry & Boucot 1972). One of the main aims of this work has been the actual definition of such 'lows' in terms of the evolutionary lineages. Of the two evolutionary expansions, in the Llandovery and the Ludlow, that in the Llandovery involves the establishment of some thirty genera or 'groups' from about ten to fifteen species or subspecies belonging to five or six genera in the Ashgill Series of the Ordovician: the actual origins of these groups are suggested. In the Ludlow expansion some fifteen 'genera' evolve from a very limited number of late Wenlock pristigraptids: the survival into the Ludlow of hooked monograptids of the *priodon* type such as *M. uncinatus* is difficult to explain in view of their apparent absence in much of the *ludensis* Zone and *nassa-dubius* interregnum (*nassa* Zone of some authors). An extra-geosynclinal oceanic source of much of the plankton is possible; whilst this might explain the absence of such forms at the top



of the Wenlock the mechanism would not be required elsewhere for an evolutionary story in which most of the chapters seem to be present. Rather, it is probably more correct to suppose that the whole Wenlock period represented a period of waning or at least stagnating graptolite evolution and that hooked monograptids became extremely rare, almost extinct, near its end: Ludlow monoclimacids may well have evolved independently from pristiograptids (p. 55 below) and not from *M. flumendosae*, the only *lundgreni* Zone monoclimacid known. Warren (1971) may, therefore, be correct in recording *M. aff. uncinatus orbatus* from the top of the *ludensis* Zone recognized in north Wales. Such rare occurrences in future studies might be predicted.

Evolutionary studies of Silurian and Devonian graptoloids have mostly been concerned with particular groups (e.g. Sudbury 1958) and these are discussed in the appropriate sections below. Papers of a more general synoptic nature have been attempted, such as Bulman's (1958, 1963) outlines of the evolution of the whole of the Graptoloidea including Ordovician groups. Elles' (1922) paper had a similar coverage but proposed actual lineages linking successive genera or groups. Since Elles' work the degree of refinement of both the Silurian stratigraphy and palaeontology has been considerable, and we can redefine her lineages and suggest many more based upon our own research. Essentially, however, the present account of the evolution of the Silurian and Devonian graptoloids may be regarded as an extension of Elles' approach, with more than half a century of additional information, rather than a paper of synoptic kind.

### III. ORDOVICIAN REMNANTS

1. '*Amplexograptus*' and the *Climacograptus innotatus* group. *Climacograptus innotatus* Nicholson was placed in the genus *Amplexograptus* by Lee (1963) on the grounds that the supragenicular wall is short and almost vertical, and the thecal excavations long and semicircular. The nature of the characteristic genicular 'spines' (Fig. 2) was not ascertained, but subsequently Stein (*in* Wolfart *et al.* 1968) interpreted these processes as genicular hoods. This is in accord with our own less sophisticated observations on this species which suggest that the Silurian forms of *C. innotatus* have a single, genicular, probably hood-like structure on each thecal tube. The following subspecies have been recognized to date:

- |                   |  |
|-------------------|--|
| <i>Silurian</i>   | <i>C. i. innotatus</i> Nicholson ; <i>acuminatus-gregarius</i> Zones<br><i>C. i. exquisitus</i> Rickards ; <i>atavus</i> Zone<br><i>C. i. jordaniensis</i> Stein ; <i>gregarius-convolutus</i> Zones<br><i>C. i. braziliensis</i> Ruedemann<br><i>C. i. obesus</i> Churkin & Carter ; <i>cyphus</i> Zone (= <i>C. i. innotatus</i> ) |
| <i>Ordovician</i> | <i>C. i.</i> subsp. undescribed ; Ruedemann 1947 : 428 ; highest Ordovician<br><i>C. i. pacificus</i> Ruedemann ; highest Ordovician<br><i>C. i. occidentalis</i> Ruedemann ; Fairmount Beds (? = <i>C. manitoulinensis</i> Caley)<br><i>C. i. nevadensis</i> Carter ; approximately <i>linearis</i> Zone                            |

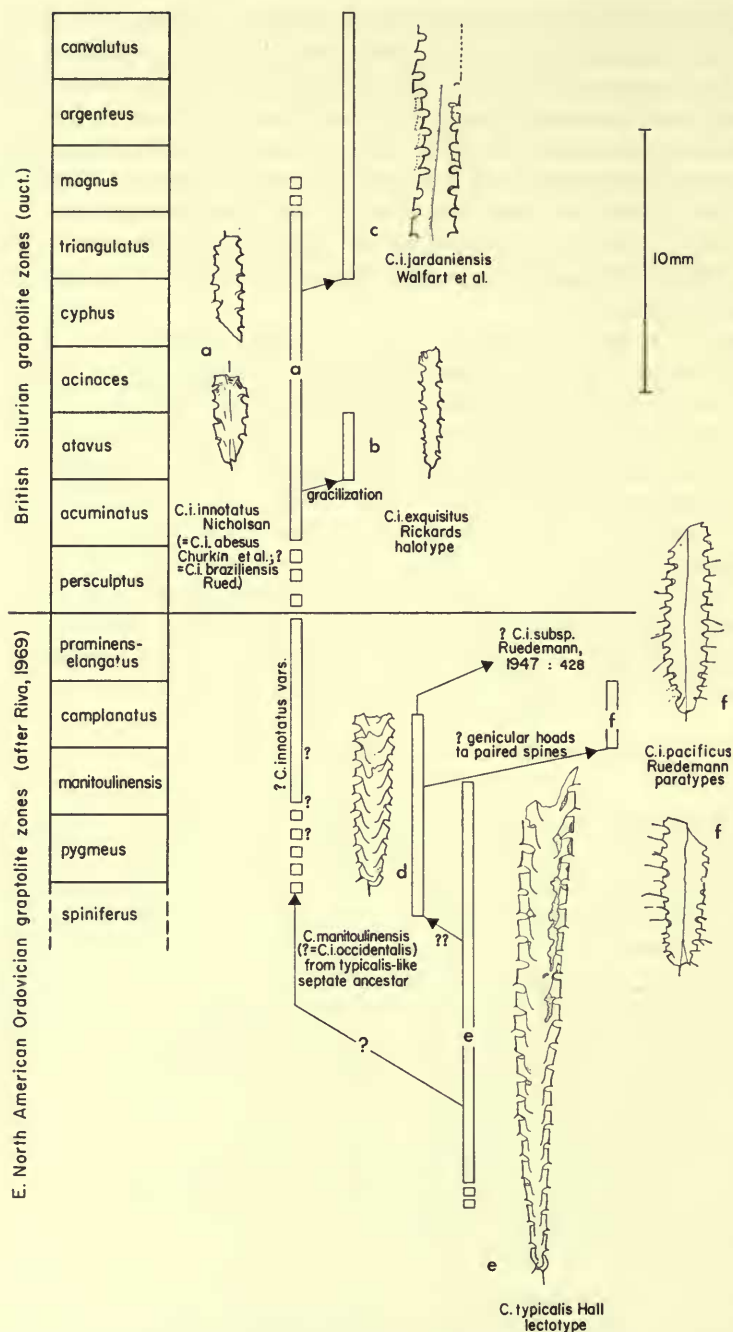


FIG. 2. Evolution of the *C. innotatus* group of species: a, LU 4019 and LU 4018; b, HUR 1Bi/126; c, after Wolfart *et al.* (1968); d, Riva Collection; e, AMNH 1090; f, USNM 1368 and unnumbered paratype.  $\times 3\frac{1}{2}$ .

The Silurian forms are mostly low Llandovery in age, and are best considered to have evolved directly from similarly specialized upper Ordovician species. *C. innotatus* itself, however, has been recorded as low as the *clingani* Zone (Churkin 1963; Churkin & Kay 1967) but there must be considerable doubt whether this is the same form: confusion with *C. manitoulinensis* or *C. i. pacificus* (Fig. 2) would be all too easy. The type material of *C. i. pacificus*, however, possibly exhibits paired genicular spines and probably not, as figured by Ross & Berry 1963 (Fig. 2 herein), a single genicular process; this leaves *C. i. occidentalis* as the only likely described ancestor since genicular spines in a biserial graptolite can be considered as extremely specialized structures with little scope for morphological change to genicular hoods.

Genicular hoods are particularly common in Silurian graptolites (*Pseudoclimacograptus*, *Monoclimacis*), but are not restricted thereto, for similar flange-like processes are found, for example, on *C. typicalis* Hall and some of its subspecies. It is possible that the *innotatus* species group has evolved from late forms of *C. typicalis* which have themselves almost amplexograptid thecae, or perhaps more probably from a *typicalis*-like septate species. However, the reference of *C. innotatus* to *Amplexograptus* by Lee (1963) is unconvincing partly because of the complete lack of amplexograptids in the uppermost Ordovician (except, possibly, *C. inuiti* Cox) but mainly because the presence of pronounced thecal processes surely sets these forms apart from *Amplexograptus* s.s. If the existence of an amplexograptid ancestor were established there would be a case for considering *C. innotatus* and its subspecies as a subgenus of *Amplexograptus*. We think it more likely that the *C. innotatus* group has evolved from a climacograptid or climacograptids by a process which had earlier produced amplexograptids, but which at such a late date involved the development of typically Silurian structures such as genicular hoods and, for biserial graptolites, small rhabdosome size (Fig. 2).

*C. innotatus* Nicholson is the type species of the monotypic subgenus *Climacograptus* (*Paraclimacograptus*) Přibyl (1947), erected to include climacograptids with thecal spines throughout the length of the rhabdosome. It is now known (Wolfart *et al.* 1968) that the thecal spines *sensu* Přibyl are, in fact, genicular hoods, and whilst his attribution recognizes the affinity of *C. innotatus* with *Climacograptus* rather than *Amplexograptus* there seem no grounds for erecting a subgenus to embrace a small climacograptid with genicular hoods. It should be emphasized that while the genicular hoods of *C. innotatus* are in all probability composed of microfusellar tissue (as in *P. (Metaclimacograptus) undulatus* Kurck) this has not yet been established.

The *innotatus* group marks the end of a minor line of evolution, and the Silurian members are typically tiny, whilst the recognized subspeciation probably involves a strong geographical as opposed to temporal element. On morphological grounds their evolutionary prospects were limited, and in many respects they paralleled the Silurian development of the pseudoclimacograptids discussed below (p. 14), a group which is also best considered as an Ordovician remnant in the Silurian and which was subjected to the changes affecting many graptolites at this time (p. 84), including the formation of genicular hoods.

2. *Pseudoclimacograptus*. Silurian representatives are few and some aspects of their evolution have been briefly discussed by Bulman & Rickards (1968) who regarded *P. (Metaclimacograptus) hughesi* (Pl. 2, fig. 2), *P. (M.) undulatus* and *P. (Clinoclimacograptus) retroversus* as late offshoots of *P. (Pseudoclimacograptus)* (Fig. 3). As with *C. innotatus* these species developed typical Silurian features: pronounced genicular hoods, specialized median septa in *hughesi* and *undulatus* and strong apertural eversion in *retroversus*. *P. orientalis* Obut & Sobolevskaya (Fig. 3b), typical of the *cyphus* and *triangulatus* Zones in the U.S.S.R., is probably a true *P. (Pseudoclimacograptus)* and may provide a link with the rare late Ordovician pseudoclimacograptids (e.g. *P. cf. clevensis* Riva 1969). Two of us (J. E. H. &

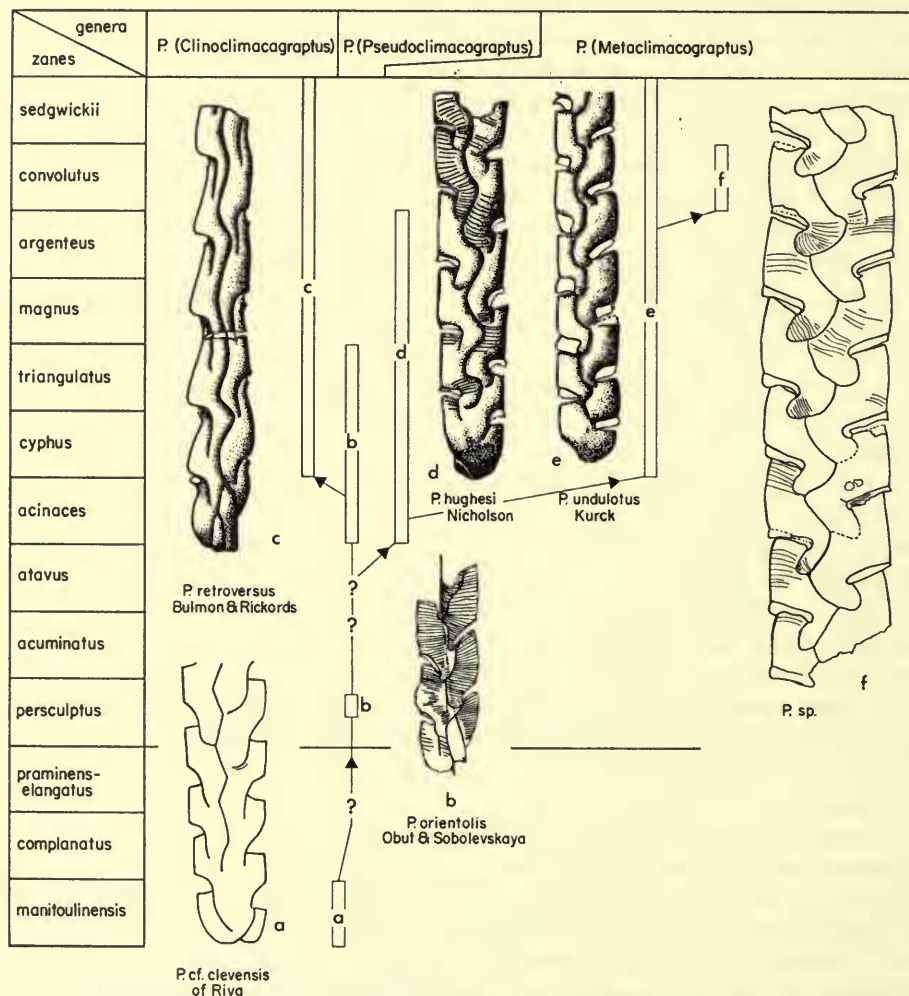


FIG. 3. Evolution of *Pseudoclimacograptus*: a, after Riva (1969); b, SM A86379; c, GSM WEG4052; d, SM A23912; e, SM A23090; f, SM A87575. All figures  $\times 14$ .



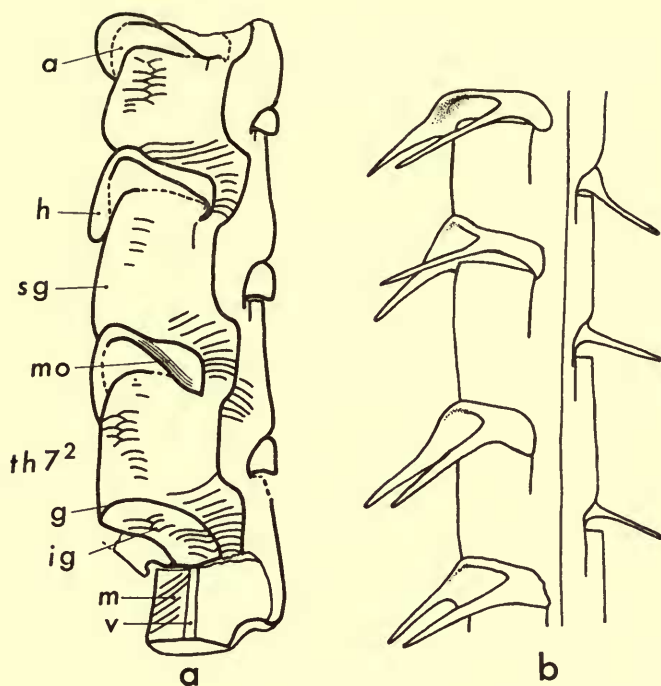


FIG. 4. a, *Pseudoclimacograptus* (*Metaclimacograptus*) *undulatus* (Kurck), SM A52953; b, hypothetical manner in which hoods of microfusellar tissue might develop paired spines. Both  $\times 40$ .

R. B. R.) have recently found *P. orientalis* in the *gregarius* Zone of Dalarne, Sweden. All the Silurian members of the genus are small compared with many Ordovician forms and, except for *P. orientalis*, show distinct Silurian characters upon a basic pseudoclimacograptid pattern (Fig. 3). The last known pseudoclimacograptids occur in the *sedgwickii* Zone.

*P. (M.) hughesi* may be intermediate between the earlier forms of *P. (P.) orientalis* and the later *P. (M.) undulatus*. This involves the development of an angular from an undulating or zigzag median septum, and an even smaller rhabdosome (0.5 mm dorsoventral width) and very close packing of the thecal tubes: indeed the angular median septum seems designed to facilitate the close packing of thecae. The pronounced genicular hoods of microfusellar tissue (Fig. 4a) on *P. (M.) undulatus* may be more strongly developed than in *P. (M.) hughesi*. The full extent of such delicate structure is often difficult to discern: nevertheless the genicular processes in Ordovician species of *Pseudoclimacograptus* seem little more than flanges.

The development of tiny pseudoclimacograptid rhabdosomes is in accord with similar diminutive rhabdosomes of the last members of other biserial groups (*Climacograptus*, *Glyptograptus*, *Orthograptus*, *Holoretiolites*), whilst the genicular hoods effectively result in the *hooked* thecal tube which, in *Monograptus* s.l., appears at the same horizon. The first known thecal hooks possibly occur in the Ordovician

*hirundo* Zone (*Atopograptus*), and definitely in post-*hirundo* strata at Port-au-Port, Newfoundland (? *Atopograptus* sp. nov., Rickards & Whittington in prep.), but in general they can be considered as Silurian morphological features which affect different groups at about the same time, beginning with *Pseudoclimacograptus* and *Monograptus* s.l. in the *cyphus* zone.

3. *Diplograptus*. This is one of the more difficult early Silurian genera to place in an evolutionary setting. Bulman (1955, 1970) points out that there is a gap in the record at the level of the highest Caradoc and most of the Ashgill; the essentially early Silurian species have proximal thecae which are more climacograptid than amplexograptid. In the uppermost Ordovician, apart from *Diplograptus modestus* (Pl. 1, fig. 4), which has a universal acme in the Silurian, we are aware of only *Diplograptus fastigatus* Davies from the British Isles. Such rare species may be the ancestors of the Silurian species, and may also originate from the earlier *Diplograptus* s.s. species, but it seems more likely that latest Ordovician and early Silurian diplograptids had their origins in either the genera *Orthograptus* and *Glyptograptus* (by proximal introduction of new characters) or in the genus *Climacograptus* (by distal introduction of new characters). In our opinion *Glyptograptus* is the most likely ancestor: whereas *Orthograptus* is a 'waning' genus in the early Silurian, *Glyptograptus* is known to have had the potential to produce species of *Climacograptus* (Packham 1962) and other graptolite genera by increasing the sharpness of the geniculum. On the other hand, *Glyptograptus* itself becomes all but extinct in the Ashgill, being represented by very few species.

In fact, although typical of the low Silurian Zones of *persculptus* and *acuminatus* and thereafter surviving into the *magnus* Zone, there is only a small number of Silurian species of *Diplograptus*: *D. modestus* Lapworth (and subspecies *parvulus*, *tenuis*, *applicatus*), *D. diminutus* Elles & Wood (Pl. 1, fig. 6), *D. elongatus* Churkin & Carter, *D. magnus* H. Lapworth (Pl. 3, figs 1 & 5; Pl. 4, figs 1 & 2), *D. ? rarus* Rickards, *D. thuringiacus* Stein, *D. fezzanensis* Desio, *D. africanus* Legrand. We have been unable to recognize any genera with an entire periderm which may have been derived from these diplograptids, whilst relationships within the diplograptids themselves have hitherto proved impossible to unravel, although Legrand (1970) convincingly demonstrated the derivation of *D. fezzanensis*, with its almost petalograptid distal thecae, from *D. africanus*.

The Silurian diplograptids are, therefore, best regarded as a quite small group of Ordovician remnants, with low evolutionary potential, which had their origins late in the Ordovician probably through rare representatives of the genus *Glyptograptus*. It is important to add that knowledge of the group is poor, and the possibility remains that they may have originated through a genus such as *Climacograptus* with a more complex thecal type than *Glyptograptus*.

4. *Climacograptus*. Unlike *Pseudoclimacograptus* other climacograptids are well represented in the late Ordovician and early Silurian (Fig. 1), enjoy something of an expansion from the *acuminatus* to the *triangulatus* Zones, and are finally represented by a single species *Climacograptus nebula* (Toghill & Strachan) from the

upper *turriculatus* to *griestoniensis* Zones inclusive. However, Jaeger (personal communication) found a stratigraphically quite isolated occurrence of *Climacograptus* sp. from the Devonian rocks of the Carnic Alps: W. B. N. B. examined specimens of it and J. E. H. and R. B. R. have examined good photographs of the specimens in question and are quite convinced of their authenticity, but have no reasonable interpretation of its presence some 40 million years after *C. nebula*. Professor Urbanek (personal communication) informs us that some Devonian monograptid populations, in his isolated Polish material, occasionally have biserial specimens, or partly biserial specimens; thus such occurrences may represent other instances of Jaanusson's (1973) dithyrial populations (see p. 38).

*C. normalis* Lapworth (Pl. 2, fig. 3; Pl. 3, fig. 4) and *C. miserabilis* Elles & Wood probably both occur in the highest Ordovician rocks, together with *C. supernus*

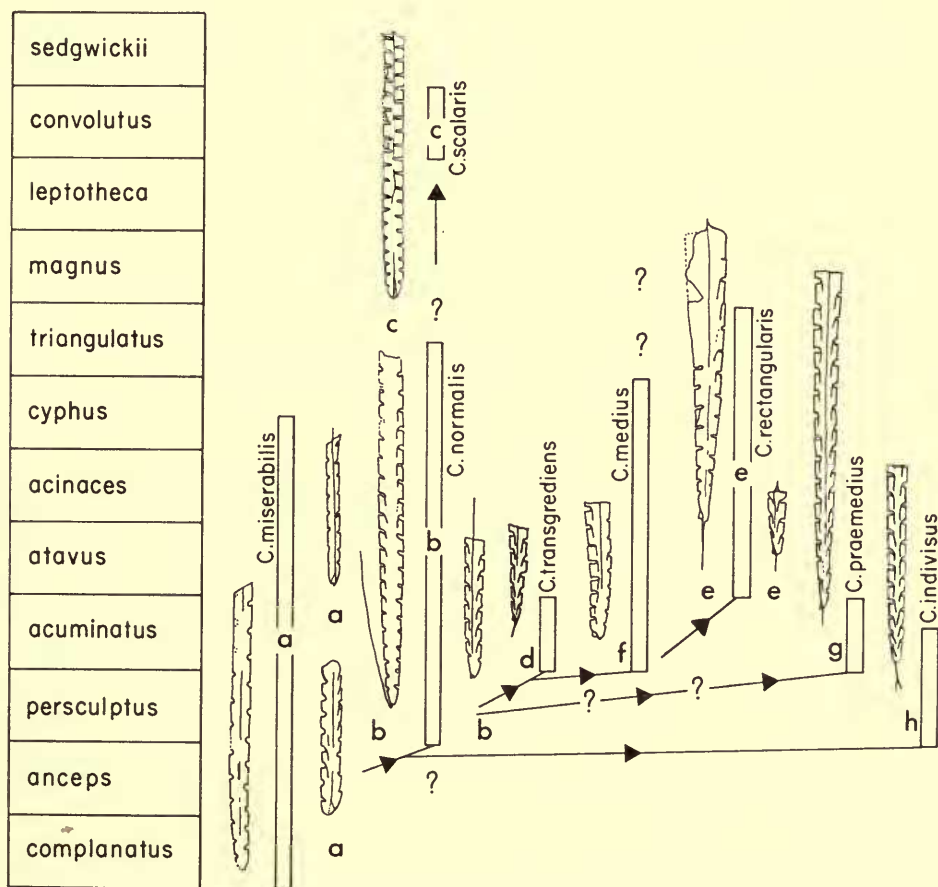


FIG. 5. Evolution of *Climacograptus*: a, BM(NH) Q2891, HUR S5-9/125 and BM(NH) Q2867; b, HUR 2Bi/96, and after Waern (1948); c, Riksmuseum Cn 1040; d, after Waern (1948); e, HUR S9-13/103, and after Waern (1948); f-h, after Waern (1948). All figures  $\times 2\frac{1}{2}$ . [*praemedius* should read *premedius*.]

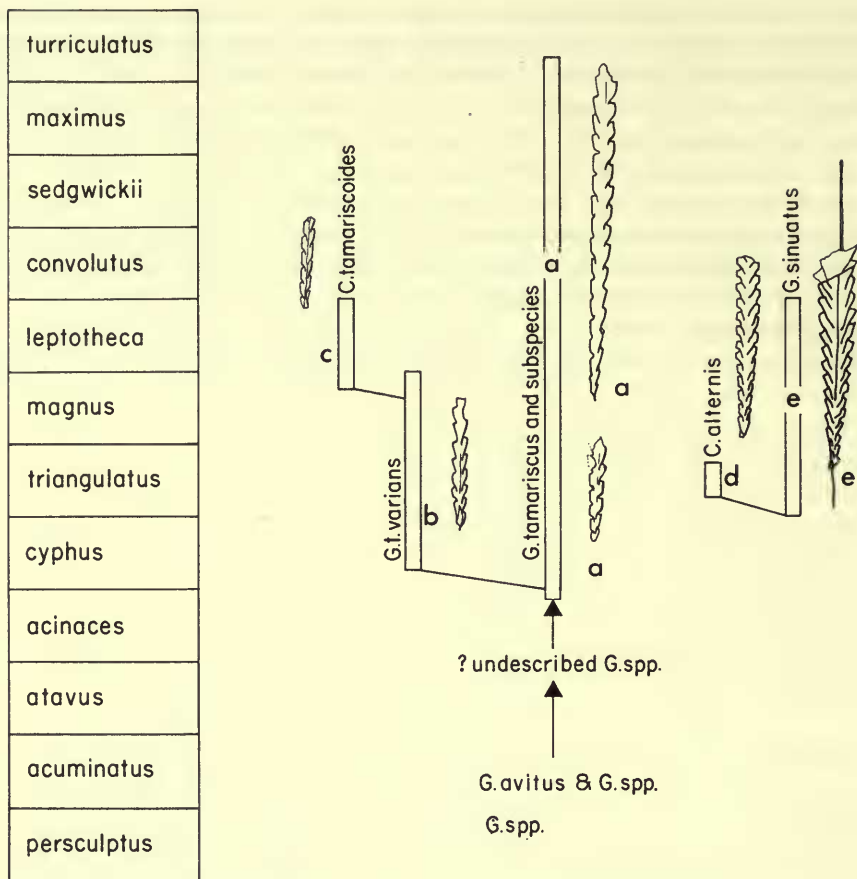


FIG. 6. Evolution of *Glyptograptus* and some *Climacograptus* species from glyptograptids; a, Scottish Geological Survey 5619 and BM(NH) 24953; b, SM A51435; c, SM A24924; d, SM A24957; e, HUR 6Bi/30. All figures  $\times 2\frac{1}{2}$ .

Elles & Wood, *C. latus* Elles & Wood and *C. hvalross* Ross & Berry. *C. normalis* and *C. miserabilis* persist into the Silurian and undoubtedly gave rise to a number of other species such as *C. rectangularis* McCoy, *C. medius* Törnquist (Pl. 1, fig. 5), *C. scalaris* (Hisinger), *C. premedius* Waern, *C. transgrediens* Waern and *C. indivisus* Davies. There are several other climacograptid species in the lower Llandovery indicating a sharp expansion from the four to six species typical of the highest Ordovician.

Some suggested evolutionary lineages have been published for these early Silurian climacograptids. Davies (1929) considered *C. miserabilis* to have evolved into *C. normalis* and *C. medius* (Fig. 5), whilst Waern (1948) established convincingly the lineage *C. normalis*  $\rightarrow$  *C. transgrediens*  $\rightarrow$  *C. medius*. In this latter line later forms have a tendency to enclose more of the sicula in the early thecae, the dorso-ventral width in general increases, the thecae become more closely spaced and the



median septum is progressively delayed (Fig. 5). In addition to this line Waern thought that *C. premedius*, *C. indivisus* and *C. rectangularis* might also have been derived from *C. normalis*.

The distinction of Silurian climacograptids from glyptograptids is not always easy (Packham 1962) and usually an arbitrary distinction is made whereby the supragenicular wall in climacograptids is more or less long and vertical and the infragenicular wall inclined at more than  $45^\circ$  from the vertical. It is possible that evolutionary links occur between the two genera (Packham 1962: fig. 6; and see Fig. 6, p. 18) and if this is correct then it implies that there are two basic groups of Silurian climacograptids: those derived from the *C. miserabilis* stock which retain vertical supragenicular walls, and those derived from Silurian *Glyptograptus* species such as *G. tamariscus varians* which acquire them. The latter group includes just those species in which the supragenicular wall may be not quite vertical (*C. alternis*, Fig. 6) and the infragenicular wall dubiously more steeply inclined than  $45^\circ$ . Thus *Climacograptus* includes species which are essentially Ordovician remnants, albeit with a Silurian expansion, and those which betray the vigour of the glyptograptid evolutionary stock in the Silurian.

#### IV. SILURIAN BISERIAL GRAPTOLOIDS AND DERIVATIVES

##### A. Groups with periderm entire

5. *Akidograptus ascensus*. Some groups in the early part of the Silurian derived from biserial graptolites are typified by protraction of the proximal regions, either by elongation of the early thecae and sicula ('*Akidograptus*') or by omission of one of the thecal series at the proximal end ('*Dimorphograptus*'). Unlike *Glyptograptus* or *Orthograptus*, from which a number of derivatives can be identified, *Climacograptus* probably gives rise only to *Akidograptus ascensus* Davies, the type species of the genus. It is characterized (Fig. 7) by distinctly climacograptid thecae and an extremely elongate sicula and thecae. No truly dimorphograptid condition is reached and the thecal sequence  $1^1$ ,  $1^2$ ,  $2^1$ ,  $2^2$  etc. can be recognized. Bulman (1932, 1936), however, considered that a shortened and vestigial  $thr^2$  'seems to be present in the genotype' (1936: 23). This, coupled with shortening of  $th2^2$ , resulted in an apparently normal sequence of thecae even though the proximal end



FIG. 7. *Akidograptus ascensus* Davies, LU 57528, Yewdale Beck, Lake District; specimen somewhat broadened by compression, to show climacograptid thecae of genus.  $\times 10$ .

was somewhat drawn out. Bulman (personal communication) was later less certain of this observation, but one of us (R. B. R.) has examined the type specimens and tends to support Bulman's earlier conclusions.

It is shown below that *Rhaphidograptus toernquisti* is derived from a subspecies of *Glyptograptus persculptus* and as far as we are aware there are no other akidograptids, raphidograptids or dimorphograptids which, because of their climacograptid-like thecae, might be supposed to originate from species of the genus *Climacograptus*.

6. *Glyptograptus*. Like *Diplograptus*, this became almost extinct in the highest Ordovician and we are aware of only *G. nicholsoni* Toghill amongst described species, although there are several undescribed, uncommon forms in both the highest Ordovician rocks (e.g. *G. n. spp.* of Riva 1969) and the *persculptus* to *acinaces* Zones in the Llandovery. There is considerable expansion of the genus in strata following the *acinaces* Zone of the Silurian, both in number of species and of specimens, but the final record seems to be that of *G. ex gr. fastigans* Haberfelner (Hutt, Rickards & Skevington 1970) from the *turriculatus* Zone of the upper Llandovery. We prefer to place *G. nebula* Toghill & Strachan (1970), which ranges into the *griestoniensis* Zone, in the genus *Climacograptus*. This decision does, however, exemplify a real difficulty with the Llandovery glyptograptid-climacograptid plexus: the mid-Llandovery glyptograptid expansion was studied by Packham (1962) who attempted to deduce evolutionary lineages, emphasising the (often) arbitrary distinction between *Climacograptus* and *Glyptograptus*. His decision, which has been largely followed by subsequent workers, was to place species in *Climacograptus* if the supragenicular wall was more or less vertical and the infragenicular wall inclined to the axis at an angle greater than 45°. Such a process necessitates the derivation of *C. tamariscoides* from *G. tamariscus varians* (Fig. 6) and makes Silurian climacograptids a polyphyletic group: earlier climacograptids were certainly derived from upper Ordovician ancestors of the *C. normalis* type.

Unlike *Climacograptus* and *Diplograptus* the genus *Glyptograptus* had tremendous evolutionary potential and probably gave rise to the early monograptids (Rickards & Hutt 1970) which in turn led to at least the bulk of monograptids, including *Monograptus*, *Monoclimacis* and *Pristiograptus*; see later sections. The divergence of glyptograptids began in the *cyphus* Zone (Packham 1962: fig. 6) after a *persculptus* Zone to *acinaces* Zone period where they were represented by very few species and mostly rare specimens. In the Llandovery, in addition to the *tamariscus* group and derivatives studied by Packham, were *G. s. sinuatus* (Nicholson) and its successor *G. s. crateriformis* Rickards (Figs 8d, c), *G. cuneatus* Rickards, *G. nikolayevi* Obut & Sobolevskaya, *G. tariti* Legrand and others probably also only distantly related to the *tamariscus* group. Whilst Packham was able to erect a convincing lineage for the well-represented *tamariscus* group the problem with the remaining glyptograptids is their sporadic and relatively rare occurrence. Thus *G. persculptus* (Pl. 2, fig. 4) occurs in the highest Ordovician rocks and in the *persculptus* Zone with *G. sp.* (Rickards & Hutt); the *acuminatus* Zone has *G. avitus* Davies and *G. sp. 1* of Rickards (1970).

Packham (1962 : 523 *et seqq.*) suggested a derivation of the whole *G. tamariscus* group from *G. avitus*. Within the *tamariscus* group itself three lineages were distinguished, each leading from *G. tamariscus tamariscus*, which as forms A, B and C span the *acinaces* to *turriculatus* Zones :

1. *G. t. tamariscus* A  $\rightarrow$  *G. tamariscus linearis*  $\rightarrow$  *G. serratus barbatus*, involving increasingly robust rhabdosomes, probably lengthening of  $\text{thr}^1$ , and development in the end member of sicular, genicular and other thecal spines or processes.

2. *G. t. tamariscus* A  $\rightarrow$  *G. t. varians*  $\rightarrow$  *C. tamariscoides*, involving probable decrease in the length of  $\text{thr}^1$ , and increased geniculation to the extent that Packham places the end member of the lineage in the genus *Climacograptus*.

3. *G. t. tamariscus* A  $\rightarrow$  *G. t. acutus*, involving possible decrease in the length of  $\text{thr}^1$  and increased geniculation, but with variable thecal spacing from one member to the next.

*G. s. sinuatus* and *G. s. crateriformis* succeed and are similar in many respects to the *G. persculptus* plexus, and we note that *G. sinuatus* is often difficult to distinguish, in the distal regions, from *Rhaphidograptus toernquisti* (Elles & Wood) which we contend (p. 24) evolved also from a member of the *persculptus* plexus. *G. nikolayevi* (*acinaces* Zone) is a possible morphological and stratigraphical intermediate between *G. persculptus* and *G. sinuatus*, which latter appears as early as the *cyphus* Zone (Rickards 1970 : 43).

The few remaining species of Silurian glyptograptids, and the small number of undescribed species at certain horizons, are in need of considerable study before evolutionary relationships can be suggested. In succeeding sections (7-10, pp. 21-25 ; 20, pp. 36-39) the relationships of glyptograptids to other genera and subgenera are discussed.

7. *Glyptograptus* (*Pseudoglyptograptus*). The subgenus was erected by Bulman & Rickards (1968) to include glyptograptids with a pronounced concavoconvex supragenicular wall and slightly everted apertural regions (Fig. 8). Subsequent work was carried out by Rickards (1972) and Rickards & Koren' (1974) so that the subgenus is now represented by the following forms :

*G. (P.) vas* Bulman & Rickards ; *magnus* Zone

*G. (P.)* sp. 1 Rickards ; exact horizon not known

*G. (P.)* sp. 2 Rickards ; *magnus* Zone

*G. (P.) rhayaderensis* Rickards & Koren' ; *triangulatus* Zone (= *G. (P.)* sp. 3 Rickards)

*G. (P.) tabukensis* Rickards & Koren' ; *convolutus* Zone

The last two species exhibit sicular spinose bundles (Rickards & Koren' 1974) not unlike that seen in *G. serratus barbatus* and '*Comograptus*' *comatus* Obut & Sobolevskaya. Further work on three-dimensional material will be required to decide whether these species also belong in *G. (Pseudoglyptograptus)*.

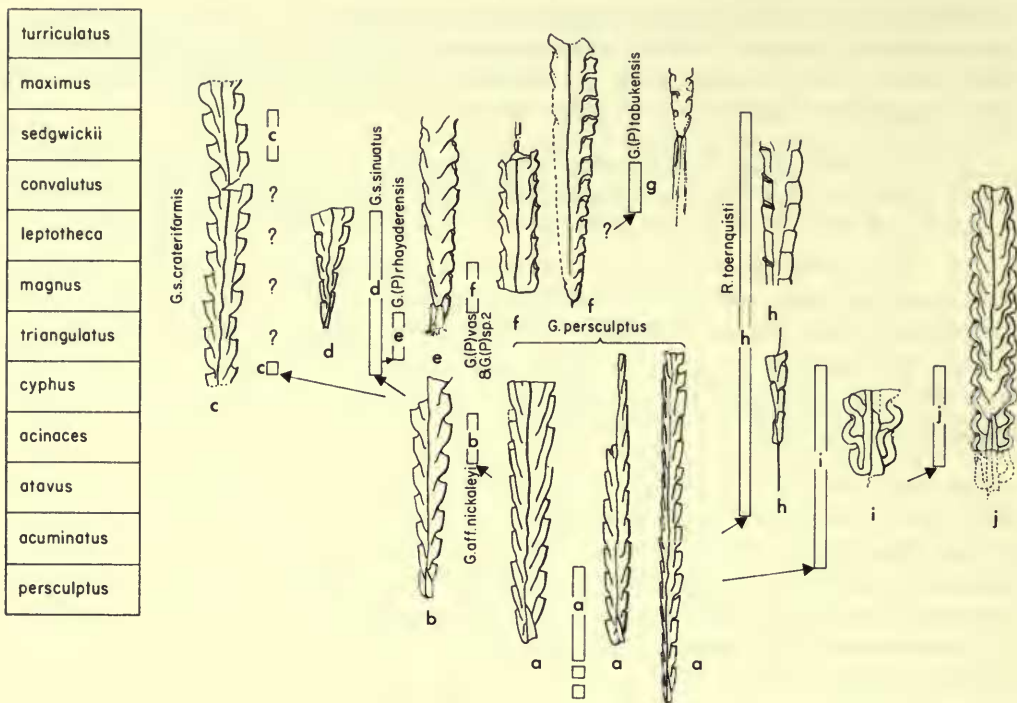


FIG. 8. Evolution of *G.* (*Glyptograptus*), *G.* (*Pseudoglyptograptus*), *Rhaphidograptus* and *Cystograptus*: a, from the left, SM A20413, SM A10012 and SM A10010; respectively Pumpsaint, Torver Beck and Dobb's Linn, showing the considerable degree of variation exhibited by *G. persculptus* populations; b, LU 4043; c, HUR S75.9.4/74; d, LU 4049; e, BM(NH) Q1583; f, BM(NH) Q1594; g, SM A81977; h, LU 57544 and, below, LU 57543; i, LU 4098; j, SM A23607. All figures  $\times 3\frac{1}{2}$ . ['aff. *nickoleyi*' should read 'aff. *nikolayevi*'].]

While it is not possible to be very certain of their evolutionary origins with respect to particular species, the general resemblance of *G. (P.) vas* to *G. sinuatus* is striking (Fig. 8), and the latter first appears earlier. Such a lineage would involve acquisition of a concavoconvex supragenicular wall, apertural eversion and, further, an upright ventral apertural process in some species (Fig. 8). Increasingly sigmoidal

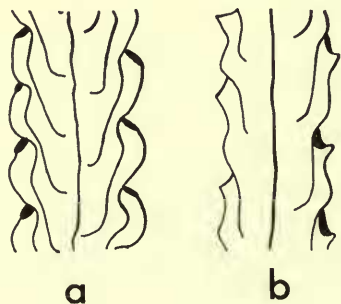


FIG. 9. Comparison of the distal thecae of *Cystograptus penna* (Nicholson), a, SM A23607, *acinaces* Zone, with *Glyptograptus* (*Pseudoglyptograptus*) *vas*, b, GSM WEG 4058, *magnus* Zone. Both figures  $\times 10$ .



thecal tubes is a feature of many Silurian graptoloids (e.g. *Cystograptus*) as is thecal eversion (*Monograptus*, *Monoclimacis* etc.), but the combination of some eversion with an upright ventral apertural process, effectively a feature of *introversion*, is unusual and can only be paralleled to a slight extent by *Pribylograptus* (Fig. 17).

*G. (P.)* spp. 1 and 2 are closely similar forms from succeeding horizons and are doubtlessly related, whilst *G. (P.) rhayaderensis* is a striking aseptate form possibly related to *G. (P.) vas* (Fig. 8). We are unable to suggest any evolutionary relationships at present for *G. (P.) tabukensis*, which is known only from Saudi Arabia.

8. *Dimorphograptus* ('*Dimorphograptus*'). Dimorphograptids *sensu lato* include forms with three different thecal types; broadly, climacograptid, glyptograptid and orthograptid. The first is now embraced by the genus *Rhaphidograptus* Bulman, although it will be shown below (p. 24) that the type species *R. toernquisti* (Elles & Wood) (Pl. 1, figs 1-2; Pl. 2, fig. 1) probably evolved from a particular glyptograptid species. The detailed thecal structure of the other two dimorphograptid types is a little uncertain, but it is at least quite clear that they are not *simply* of glyptograptid or orthograptid type (Fig. 10). Bulman (1970) has pointed out that some forms show apparent apertural isolation, a typically Silurian evolutionary feature (p. 91), while others show undulating and possibly more complex thecal apertures (Fig. 10). It is also possible that strictly orthograptid thecae are absent in these groups and that they are all basically glyptograptid.

However, it is not unreasonable to suppose that *D.* ('*Dimorphograptus*') types, with broadly glyptograptid thecae, evolved from one or more species of *Glyptograptus*, or that *D.* ('*Bulmanograptus*'), with orthograptid thecae, evolved from *Orthograptus* (but see p. 28). The type species of *Dimorphograptus* is *D. elongatus* Lapworth (Pl. 1, fig. 3), which has a long uniserial portion and glyptograptid thecae, and, like other dimorphograptids *sensu lato* (except *Rhaphidograptus*), has the initial bud upwardly directed at its origin. The distal portions of the rhabdosome (Fig. 11) are indistinguishable from *Glyptograptus*.

Bulman (e.g. 1970) has discussed the development of a uniserial from a biserial rhabdosome and this will not be further discussed here except to note that loss or reorientation of  $th1^2$  is necessary as well as a septate rhabdosome. Since dimorphograptids are preceded in the record by *M. ceryx* Rickards & Hutt they are probably best regarded not as evolutionary intermediates between biserials and uniserials, but as biserials which have been partially affected by Silurian evolutionary trends

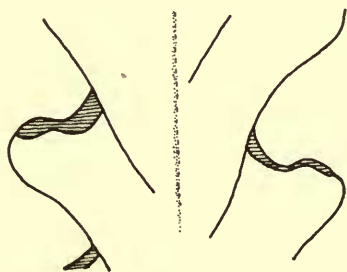


FIG. 10. Diagrammatic sketch of thecae of *Dimorphograptus* sp., GSM, from Bryn Dowski borehole at 119.10 m, *cyphus* Zone; illustrating undulating thecal aperture.  $\times 20$ .

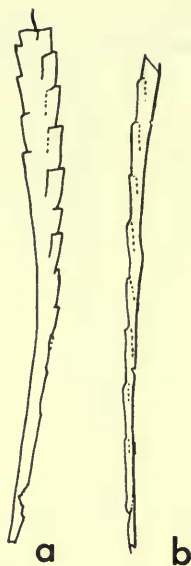


FIG. 11. *Dimorphograptus elongatus* Lapworth. a, LU 57506; b, LU 57507, School Beck, Lake District, *atavus* Zone. Both figures  $\times 5$ .

including thecal isolation and growth of genicular hoods (p. 91) as well as partial production of a uniserial rhabdosome. It is noteworthy that the successful and quite rapid introduction of a new character in one graptoloid group is quite often followed by similar but apparently abortive introduction in another. In this case the environmental pressures resulting in the uniserial rhabdosomes must have waned shortly afterwards, since there is no evidence at all that uniserial graptoloids were again to develop from biserial ancestors: the waning period was effectively the time span of the *acuminatus* and *atavus* Zones during which the genera *Rhaphidograptus*, *Dimorphograptus sensu lato* and *Akidograptus* appeared. No *Dimorphograptus* species appear after the *cyphus* Zone, and very few rhabdigraptids, but there is a tendency to protraction of the proximal end of biserials even as late as the *convolutus* Zone (p. 88 below).

9. *Rhaphidograptus*. The genus as originally defined included only *Climacograptus toernquisti* Elles & Wood, but the definition has since been extended by its author (Bulman 1955, 1970) to include dimorphograptids with climacograptid thecae. Thus *D. extenuatus* Elles & Wood, the type species of *Metadimorphograptus* (Přibyl 1948), is now included. Whilst it is quite reasonable that rhabdigraptids should have evolved from *Climacograptus* by a parallel of the same tendencies affecting glyptograptids, we nevertheless note the great difficulty in distinguishing distal thecae of *R. toernquisti* from those of *G. sinuatus* and *G. persculptus*. We prefer, in fact, to derive *R. toernquisti* from a slender form of *G. persculptus* (see Fig. 8), the biserial portions of which seem quite identical to that of *R. toernquisti*.

Both *R. toernquisti* and *R. extenuatus* appear in the *atavus* Zone, the latter, with its longer uniserial portion, somewhat earlier in the Lake District than

*R. toernquisti*. The following species have been recorded at the same and higher levels by Obut & Sobolevskaya (1967, 1968) : *R. ? vicinus* Obut & Sobolevskaya ; *R. maslovi* Obut & Sobolevskaya ; *Agetograptus secundus* Obut & Sobolevskaya ; *A. primus* Obut & Sobolevskaya ; *A. zintchenkoae* Obut & Sobolevskaya. Of these *A. zintchenkoae* and *R. maslovi* have thecae which are more obviously glyptograptid, while *A. secundus* may represent the occurrence of the rhabidograptid condition in a species of orthograptid origin. One of us (R. B. R.) has examined the originals of all these Russian species and is of the opinion that with *R. toernquisti* and *R. extenuatus* they represent a group with glyptograptid ancestors, in which greater geniculation has occurred than in the derivatives *D.* ('*Dimorphograptus*') and *D.* ('*Bulmanograptus*'). It should be added that in any bedding plane with numbers of specimens of *A. secundus* some will have the long (rhabidograptid) thr<sup>2</sup> while others will be of normal biserial type : another case of Jaanusson's (1973) dithyrial populations (p. 38).

10. *Cystograptus* Hundt (1942) was emended by Jones & Rickards (1967), who suggested that the type species had the same double sigmoid (ogee) thecal curvature as *C. penna* which was studied in three-dimensional material. Teller (1969) presumably did not accept the suggestion but one of us (J. E. H.) later obtained Lake District specimens of *C. vesiculosus* (Fig. 8i, p. 22 ; Pl. 2, fig. 7) conclusively demonstrating the ogee curvature. As far as we are aware no other cystograptids have been described, but Mu & Lee (1958) describe apparently identical thecal structures in *Glyptograptus ? curvithecatus* Mu & Lee from the *hirundo* Zone of west Chekiang. It is possible that some mistake in horizon or locality has been made by Mu & Lee, although the claimed associated fauna is undoubtedly Arenig.

Fig. 9 depicts a possible morphological relationship between *Cystograptus* and *G.* (*Pseudoglyptograptus*). Continued growth of the thecal tube over the geniculum of the latter genus would result in the genus *Cystograptus*. Such an evolutionary relationship is precluded by the early appearance of *Cystograptus* (*acuminatus* to *cyphus* Zones), but the derivation of both genera from *Glyptograptus* seems likely : a member of the *G. persculptus* plexus seems a possible contender as the ancestor of *C. vesiculosus* (Fig. 8).

The main Silurian tendencies displayed by *Cystograptus* are, therefore, the thecal elongation and apertural eversion. The pronounced nemal vanes (Jones & Rickards 1967) occur in some form in a number of Silurian biserial groups and it is possible that the number of species possessing them greatly exceeds that in the Ordovician : development of vanes is probably dominantly a Silurian tendency of which one of the first representatives is *Cystograptus*.

11. *Orthograptus*. The genus is quite well represented in the late Ordovician by various forms of *O. truncatus* Lapworth (Pl. 1, fig. 7), which species also persists rarely into the *acuminatus* Zone of the Silurian. Within the Silurian, however, orthograptids are only rarely represented by more than one or two species in any one zone, and each species usually forms only a small proportion of the graptoloids



encountered. In the Howgill Fells, for example, Rickards (1970) collected only about twenty specimens of *Orthograptus* whilst Hutt (1974) recorded only ninety specimens from a collection of some 20,000 Llandovery graptoloids. The genus is discussed here, rather than as an 'Ordovician remnant', since it may well have given rise directly to three further groups or genera (sections 12-14 below), and ultimately to all the retiolitid genera (sections 16-19 below).

Evolution within *Orthograptus* itself is difficult to discern for the same reasons that apply to *Diplograptus*, namely paucity of species and specimens. Neither Toghill (1968a, b) nor Hutt (1974) record *Orthograptus* from the *persculptus* Zone, but both identified *O. truncatus abbreviatus* Elles & Wood in the *acuminatus* Zone. Hutt in addition regards *Akidograptus acuminatus* (Nicholson) as an orthograptid with a protracted proximal region, an interpretation with which all the present writers agree (p. 28). The only record in beds possibly partly equivalent to the *atavus* Zone is *O. eberleini* Churkin & Carter from Alaska, whilst the succeeding orthograptids appear in the following order: *O. mutabilis* (*acinaces* and *cyphus* Zones), *O. cyperoides* and *O. bellulus* (*triangulatus* to *sedgwickii* Zones), *O. obuti* (*triangulatus* Zone), *O. insectiformis* (*magnus* to *convolutus* Zones).

*O. eberleini* is a diminutive species with a small sicula, but *O. mutabilis* has the long free sicula and proximal end typical of the succeeding *O. cyperoides* and *O. insectiformis*. Hutt (1974) has shown that, like *O. insectiformis*, *O. cyperoides* and *O. bellulus* also have thecal spines albeit somewhat more slender than in *insectiformis*, which also exhibits a strongly divided virgella in the form of a meshwork (Hutt 1974; Rickards & Koren' 1974). It is very likely that *O. mutabilis*, if not *O. eberleini*, gave rise to *O. cyperoides*, *O. bellulus* and then to *O. obuti* and *O. insectiformis* by development of increasingly long and robust thecal spines. The last species to appear, *O. insectiformis*, develops a virgella meshwork, as does *O. obuti* Rickards & Koren' (*triangulatus* Zone of the southern Urals). Fig. 12 depicts the suggested simple progression which, whilst fitting the known record and morphology quite well, perhaps hides the fact that the species are not well known from three-dimensional material.

Another problem which we have no wish to avoid is the actual origin of Silurian orthograptids. It is conceivable, though unlikely, that *O. truncatus abbreviatus* gave rise to *O. eberleini* and hence to the lineages of Fig. 12. But there are no indications in either species of the *mutabilis* proximal end and they are best regarded as the last representatives of '*Rectograptus*' (Přibyl 1947). Thus it is possible that the remaining Silurian orthograptids have their origins in a Silurian genus such as *Glyptograptus*. *Glyptograptus? enodis* and *G. aff. nikolayevi* (Fig. 8), from the *cyphus* and *acinaces* Zones respectively, have proximal ends much closer to the *O. mutabilis* type. Furthermore, it is known that later glyptograptids develop thecal spines.

Finally, it is of interest that these observations on *Orthograptus* do not lend much support to Přibyl's classification of orthograptids into those with apertural spines (*Orthograptus quadrimucronatus*) and those without (*Rectograptus truncatus*): Silurian forms have previously been placed in *Rectograptus* by those workers favouring such generic distinctions.



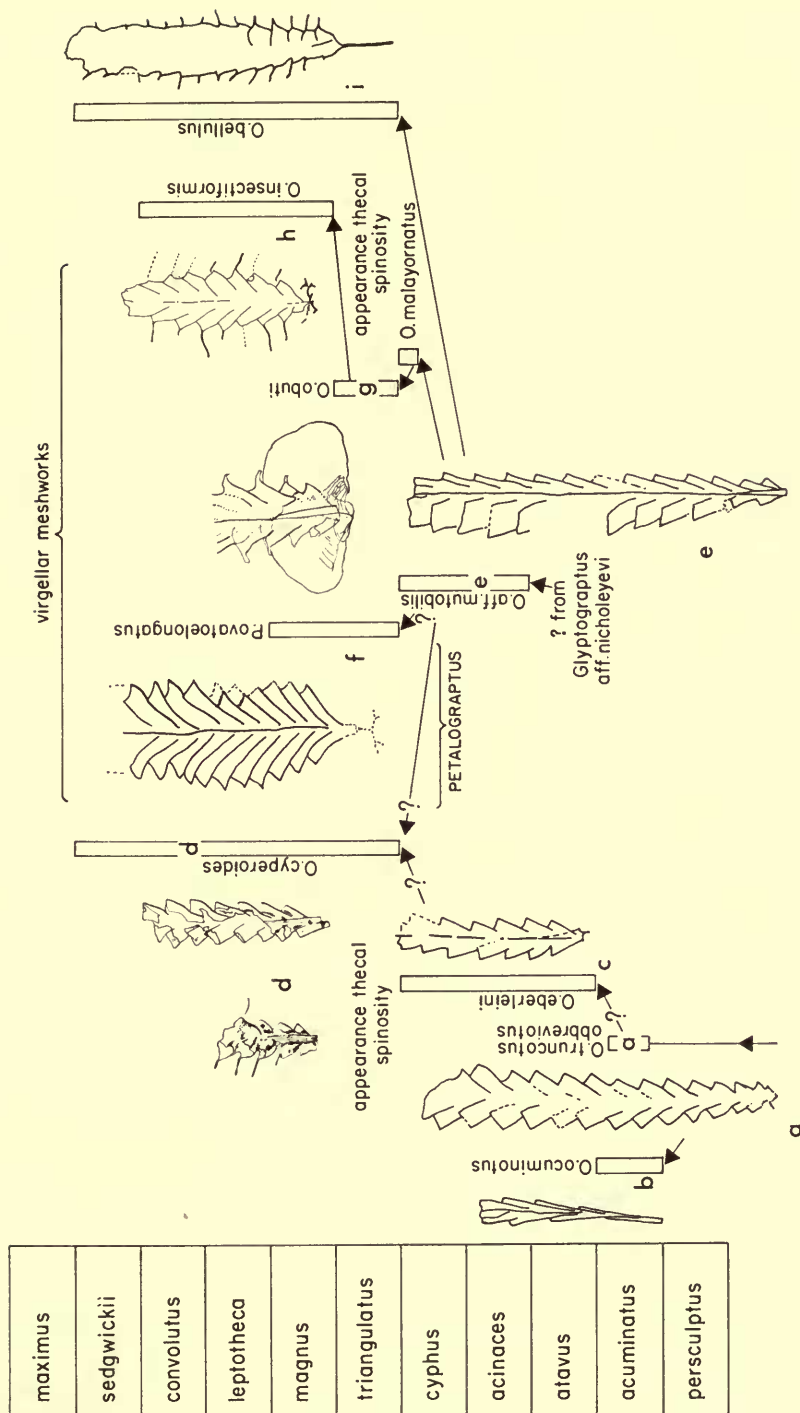


FIG. 12. Evolution of *Orthograpthus*: a, BM(NH) Q2866, *anceps* Zone; b, HUR S/1; c, USNM 161783; d, from the left, LU 4085 and LU 4081; e, LU 4074; f, LU 57537; g, after Rickards & Koren' (1974); h, BM(NH) Q3112; i, LU 4090. All figures  $\times 4\frac{1}{2}$ . ['aff. *nicholeyevi*' should read 'aff. *nikolayevi*']

12. *Orthograptus acuminatus*. This species (Pl. 2, fig. 3) is usually grouped in *Akidograptus* with *A. ascensus*, the type species of the genus which has climacograptid thecae. *O. acuminatus* has broadly orthograptid thecae but shares with *A. ascensus* a protracted proximal end and an elongated sicula except in the subspecies *O. acuminatus praematurus* Davies. This last looks like a normal orthograptid with a pointed proximal end and a slight thecal geniculation. Thus *O. acuminatus* is best regarded as an orthograptid which has assumed the typically Silurian features of elongated thecae and sicula and protraction of the proximal end. There is no uniserial portion in either *A. ascensus* or *O. acuminatus* and each resulted from similar environmental pressures exerted upon representatives of *Climacograptus* and *Orthograptus* respectively. Other species similar to *O. acuminatus* have been described: *A. zhejiangensis* Yang (1964), *A. giganteus* Yang (1964), *A. a. precedens* Münch (1952), *A. priscus* Hsü (1934); it may become desirable eventually to erect a new genus to embrace this rather unusual and stratigraphically restricted group of orthograptids, particularly in view of the fact that the thecae, although broadly orthograptid, have a slight geniculum and rather undulating, fractionally introverted thecal apertures. *A. giganteus* has climacograptid-like proximal thecae and orthograptid-like distal thecae, and may represent the imposition of the Silurian *Diplograptus* trend upon a climacograptid or glyptograptid stock (p. 16).

13. *Dimorphograptus* ('*Bulmanograptus*'). Some reference has been made above (p. 23) to these forms typified by *D. confertus* Nicholson. The thecae are certainly not of simple orthograptid type and it is far from certain that they are of orthograptid origin. Indeed we feel that much further investigation of this group of dimorphograptids is required before any firm suggestions about origins can be made. In the meantime it is noted that some species display apparently isolated thecal apertures (*D. decussatus*), a typically Silurian feature, whilst others have possibly complex thecal apertures (Fig. 10).

14. *Petalograptus*. Petalograptids range from the *triangulatus* to the *crenulata* Zone but are particularly abundant and more varied at the lower end of the range (Fig. 1). Many of the described petalograptids (e.g. *P. palmeus* (Barrande), *P. elongatus* Bouček & Přibyl; Figs 13a, b) bear close resemblance to *Orthograptus* species and it is without doubt that their origins lie within this genus: indeed these *Orthograptus* derivatives clearly fitted the new Silurian environment better than the *Orthograptus* species themselves which, as we show above (p. 26), are somewhat restricted in numbers of species and specimens.

*Petalograptus* species retain a small sicula but the proximal end nevertheless displays pronounced protraction which is achieved by strong upward growth of all the thecae except the initial bud of thr<sup>1</sup>. The great length of the thecal tubes, coupled with this upward growth, results in a foliate, tabular rhabdosome. In addition, the genus may be distinguished from *Orthograptus* by the more common nemal vanes and the gentle ventral concavity (in profile) of the thecae.

At the specific level some of the forms described by Bouček & Přibyl (1941) provide morphological intermediates: *P. elongatus* must be considered a borderline

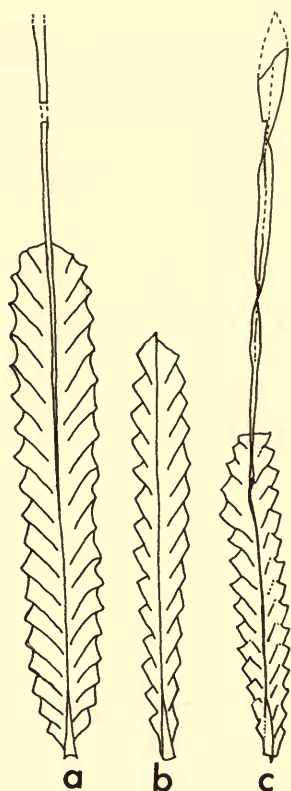


FIG. 13. Diagram indicating range of variation in *Petalograptus*. a, *Petalograptus palmeus palmeus* (Barrande) after Bouček & Přibyl (1941); b, *P. elongatus* Bouček & Přibyl (1941); c, *Petalograptus* sp. SM A75383, *crispus* Zone, Lake District; each has distinct orthograptid features and b is best regarded as a borderline petalograptid. All figures  $\times 5$ .

petalograptid. Nevertheless, some of the earliest forms such as *P. ovatoelongatus* are the most typical of petalograptids. One problem of the origin of such *triangulatus* Zone species as *P. ovatoelongatus* and *P. minor* (Pl. 2, fig. 2) is that the number of known, possible, *Orthograptus* ancestors is very limited (p. 26). *O. mutabilis* from the *acinaces* and *cyphus* Zones has a similar rhabdosomal and thecal appearance and a sicula some 2 mm in length, and must be regarded as the most likely ancestor of *P. ovatoelongatus*, which, unlike some later petalograptids, has a sicula 2 mm long at least in the Howgill Fells (Rickards 1970).

Subsequent evolution within *Petalograptus* is difficult to understand. Preliminary work by two of us (R. B. R. & J. E. H.) suggests that infraspecific variation may be rather greater than in species of contemporary genera. It is also possible that the genus is polyphyletic and that some of the slim petalograptids of higher horizons (e.g. *P. wilsoni* Hutt) may derive from some of the last orthograptids although the known species are spinose (Fig. 12). Certainly there seem to be two groups persisting throughout the range of petalograptids, the one a robust group basically resembling *O. ovatoelongatus*, the other with more slender species (Pl. 3, fig. 2) resembling *P. wilsoni*. Specific lineages within the *Petalograptus* species pose an interesting problem for future research.

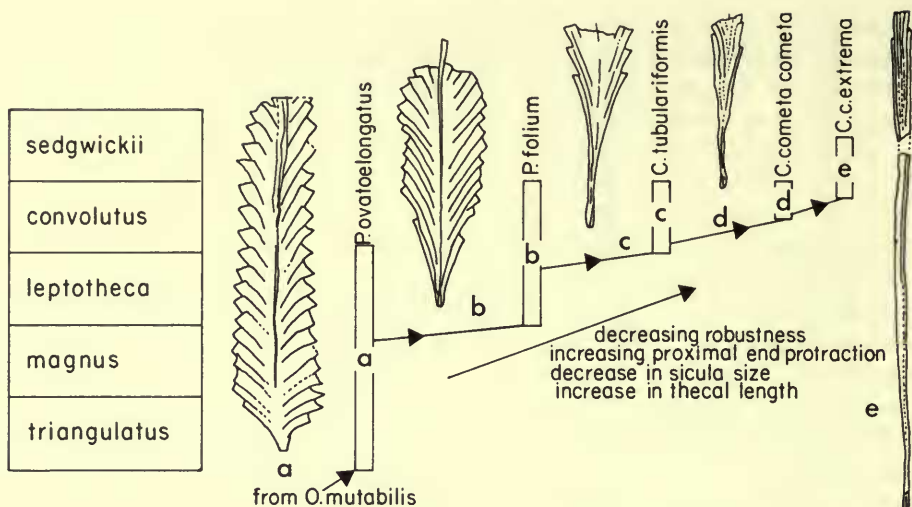


FIG. 14. Derivation *Cephalograptus* from *Petalograptus*: a, GSM CV8930; b, after Bouček & Přibyl (1941); c, BM(NH) Q102; d, LU 57546; e, LU 57551. All figures  $\times 2\frac{1}{2}$ .

15. *Cephalograptus* Hopkinson (1869) is an extreme development of *Petalograptus*, embracing few species, in which protraction of the proximal end (Fig. 14) has been carried out to such an extent that the early thecae ( $r^1$ ,  $r^2$ ) are probably the longest known graptoloid thecae. Specimens from the Lake District are known with thecae over 17 mm long whilst Elles & Wood (1908) record specimens with thecae of 30 mm length.

There is probably a stratigraphical and evolutionary succession from a form such as *P. ovatoelongatus* (*triangulatus* to *convolutus* Zone), to *P. folium* (*leptotheca* and *convolutus* Zones), to *Cephalograptus cometa* (top of *convolutus* to *sedgwickii* Zone). With the exception of *Dimorphograptus elongatus* (*atavus* Zone), which resembles an attempted monograptid, *C. cometa* may be regarded as the most extreme example of proximal end protraction, exceeding even *A. ascensus* and *R. toernquisti*. Only *C. cometa cometa* (Geinitz), *C. c. extrema* Bouček & Přibyl and *C. tubulariformis* Nicholson have been described: the species *O. acuminatus* Nicholson was placed doubtfully in *Cephalograptus* by Elles & Wood (1908) but it should be accommodated neither there nor in *Akidograptus* (p. 28); it is best considered an orthograptid with a protracted proximal region.

## B. The Retiolitids

The most spectacular gap in the record between apparently similar groups in the Ordovician and Silurian is that between the (Ordovician) Archiretiolitinae and the Silurian retiolitids *sensu lato* – which do not appear until the *argenteus* Zone. As far as we are aware no retiolitids have yet been obtained from the *anceps* to the



*magnus* Zones inclusive, which indicates a Silurian ancestry amongst the biserial graptolites for the Silurian retiolitids. Silurian retiolitids fall broadly into two subfamilies, the Retiolitinae (? *triangulatus*, ? *magnus*, *argenteus* to *centrifugus* Zones, ? *murchisoni* Zone) and the Plectograptinae (Middle Wenlock, top *riccartonensis* Zone, to post *leintwardinensis* Zone strata). These groups are discussed below in sections 16–19).

16. *Retiolites*, *Stomatograptus* and *Sinostomatograptus*. The genus *Pseudoretiolites* Bouček & Münch (1944) was included in *Retiolites* by Bulman (1970) and Hutt (1974), but here we prefer to treat it separately (section 17, p. 33) since, as defined, it spans the *argenteus* to *maximus* Zones at the most whereas *Retiolites* (restricted) first appears in the *griestoniensis* Zone (? *crispus* Zone).

*Retiolites geinitzianus* shows considerable variation in rhabdosomal form and is clearly in need of considerable revision. Forms not unlike *R. g. angustidens* Elles & Wood, a typical *centrifugus* Zone form in Britain, occur as low as the *griestoniensis* Zone in the Howgill Fells, North America and the U.S.S.R., whilst robust forms occur less commonly at the same level. The long broad forms (i.e. typical *R. geinitzianus*) bear a striking resemblance to *Petalograptus altissimus*, to such a degree in fact that they are often mistaken for each other in museum collections. The derivation of *R. geinitzianus* from *P. altissimus* would involve, however, considerable periderm reduction, the development of a clathria, and, a more difficult morphological step perhaps, the incorporation of the nema or virgula in one of the rhabdosomal lateral walls. This last step is not always taken in Silurian retiolitids (p. 36).

The recent work on the periderm ultrastructure of retiolitids (Urbanek & Rickards 1974) does not preclude such a derivation, but the clathrial ultrastructure is, as might be expected, rather specialized and extremely electron dense. Some recent work on retiolitids (Skoglund, personal communication, and 2nd Soviet Graptolite Conference in Tallin) has shown that the clathria and reticula may be underlain by a thin but complete periderm, possibly of fusellar tissue.

*Stomatograptus* and *Sinostomatograptus*, the latter recently recorded outside China for the first time (Hutt 1974; Fig. 15), are basically similar to *Retiolites* and the thecae are essentially orthograptid or petalograptid. Since orthograptids are unknown in the highest Llandovery (Fig. 12) petalograptids would seem to be the only likely ancestors to all three genera *Retiolites*, *Stomatograptus* and *Sinostomatograptus*. The supposed lacinia in the last of these requires further study, but there would seem to be no grounds at present for linking the genus with *Pseudoplegmatograptus* (Fig. 15; p. 33) rather than with *Retiolites* and *Petalograptus*. *Stomatograptus*, like the much earlier *Pseudoretiolites*, has a solid intertheatal septum but clearly in this feature cannot be regarded as very much different from those forms of *R. geinitzianus* which have a thin but continuous layer of periderm beneath the clathria and reticula. Both *Stomatograptus* and *Sinostomatograptus* have a median row of large pores, or stomata, along the lateral walls. These do not coincide with the thecae themselves and are almost certainly a strengthening feature of the reticula: those retiolitids lacking a strengthening of the lateral walls often tear



along the length of them. *Plectograptus? bouceki* Rickards (section 18 below, Fig. 16) is often found torn along its length.

There are very few species of the stomata-bearing genera, but a whole variable plexus of forms referable to *R. geinitzianus sensu lato*: the nature of this plexus needs unravelling before further specific lineages can be proposed.

17. *Pseudoretiolites* and *Pseudoplegmatograptus*. Of these two genera *Pseudoretiolites* occurs much earlier, possibly as early as the *triangulatus* Zone (Elles & Wood 1918). As well as having a solid interthecal septum we now know from isolated Swedish specimens in the collection of two of us (R. B. R. & J. E. H.) that this is composed of fusellar tissue and displays clear growth lines (Fig. 15). Further, there is an apparent genicular homologue and an almost vertical supra-genicular wall: the clathria is poorly developed, the reticula fibrous, and the nema possibly central.

The nature of the thecae suggests an origin not from *Orthograptus* or *Petalograptus* but from *Climacograptus* or *Diplograptus*. The short supragenicular wall and long excavations, as well as the dorsoventral width (up to 5 mm) and shape and size of the rhabdosome, recall *D. magnus* H. Lapworth (cf. Figs 15a, b) which may precede *P. perlatus*, although there is certainly some doubt about the first occurrence of the latter. In any event a *Diplograptus* ancestor seems a distinct possibility for *Pseudoretiolites*. The writers are aware of the following species in *Pseudoretiolites*: *P. perlatus* (Nicholson); *P. petalograptoides* Bouček & Münch; *P. thuringicus* Bouček & Münch; *P. sp.* Bouček & Münch (1952); *P. dentatus* Bouček & Münch (1944). One of these, *P. petalograptoides*, closely resembles *Petalograptus ovatus*, possibly suggesting an origin in this genus and at the same time indicating that *Pseudoretiolites* may be polyphyletic.

*Pseudoplegmatograptus* probably appears in the *sedwickii* Zone and ranges into the *crenulata* Zone. It thus overlaps with *Sinostomatograptus* which also possesses a lacinia and indistinct clathria. However, the presence of a sclerotized interthecal septum in *Sinostomatograptus* probably indicates a more recent origin from *Petalograptus*, rather than from *Pseudoplegmatograptus* which apparently lacks thecal fusellar periderm.

Because of the apparently ill-defined clathria the thecae of *Pseudoplegmatograptus* are difficult to discern, but they may be essentially of orthograptid type (Bulman 1970: fig. 95.7) with thecal spines and a supported and somewhat nebulous lacinial network. Because of the dorsoventral width up to 6 mm in most pseudoplegmatograptids such thecae must be very long and inclined to the axis of the rhabdosome at quite a high angle, at least adaperturally (Fig. 15d), perhaps suggesting a link with the petalograptids or orthograptids. Derivation from *Pseudoretiolites* seems unlikely if the structure of the latter is as illustrated in Fig. 15b. We would like to emphasize here, however, that there are probably other retiolitids to be discovered at these levels, particularly by chemical techniques (e.g. Hutt, Rickards & Skevington 1970): retiolitid structures in the rock are exceedingly difficult to distinguish. Until the structure is worked out in the same detail as in other retiolitids the origin of *Pseudoplegmatograptus* must remain a matter for speculation, but



it seems highly unlikely that it could give rise to any of the later retiolitid genera (see Fig. 15).

18. *Plectograptus*?, *Plectograptus* and *Paraplectograptus*. Following the last occurrences of *Retiolites* and *Stomatograptus* in the low Wenlock (probably in the *centrifugus* or *murchisoni* Zones; Fig. 16) there is a gap, at least equivalent to most of the *riccartonensis* Zone, where no retiolitids have been recorded. One of us (R. B. R.) has examined specimens from Podolia, possibly referable to *Plectograptus*?, provided by Dr Koren', which occur with a *murchisoni* Zone assemblage including *C. m. murchisoni*. This suggests that there are yet other retiolitids to be discovered in the low Wenlock strata. Otherwise the earliest form to appear in the Wenlock is *P. ? textor* Bouček, a species similar to the succeeding *Plectograptus ? bouceki* Rickards. The former was considered by Rickards (1967) to have orthograptid-like thecae throughout and the latter to have proximal 'climacograptid' thecae and distal 'orthograptid' thecae. Such a species as *P. ? bouceki* could, therefore, provide a link between the low Wenlock *Retiolites* (with 'orthograptid' thecae) and the upper Wenlock *Plectograptus* species (with 'climacograptid' thecae). There are no other possible ancestors from which *P. ? bouceki* could be derived, for biserials with a solid periderm became extinct with *P. altissimus* (but see p. 17), and the only biserials to survive into the low Wenlock are referable to *Retiolites* or *Stomatograptus*. These latter may, therefore, have given rise to the Podolian species, or to *P. ? bouceki*, and the whole relatively successful development of late Wenlock, low Ludlow retiolitids hinges upon this group.

*Plectograptus* (Fig. 16c) has a central nema and in this respect contrasts with *Retiolites*. Since *Retiolites* must have acquired its laterally positioned nema from an ancestor with a central nema (p. 31) the reversion to the earlier condition seems odd and is a feature not usually encountered in the evolution of the graptoloids. In *Plectograptus* ? the position of the nema is uncertain. However, as will be shown below, the position of the nema with respect to the lateral rhabdosomal wall is rather variable in the late Wenlock and low Ludlow retiolitids. On present evidence one cannot select a postulated lineage which does not require the nema to change its position at least twice.

*Paraplectograptus* Přibyl, from the *lundgreni* Zone, has the appearance of a much simpler *Plectograptus* (Fig. 16f) but with the nema embedded in a lateral rhabdosomal wall. The only immediate ancestors of *Paraplectograptus* are species of *Plectograptus* and *Plectograptus* ? which have a central nema. The derivation of *Paraplectograptus* from *Plectograptus* involves loss of the parietal lists, one of the ? subapertural loops, and the list connecting the ? subapertural and ? genicular lists (Fig. 16f).

19. *Gothograptus*, *Holoretiolites* and *Spinograptus*. *Gothograptus nassa* Holm appears in the top of the *lundgreni* Zone, and like *Plectograptus* has a 'climacograptid' appearance with a geniculum (armed with a genicular hood) and a supragenicular wall, defined by clathrial and reticular elements, which slopes slightly inwards towards the next aperture. The nema is at first central, as in *Plectograptus*, but



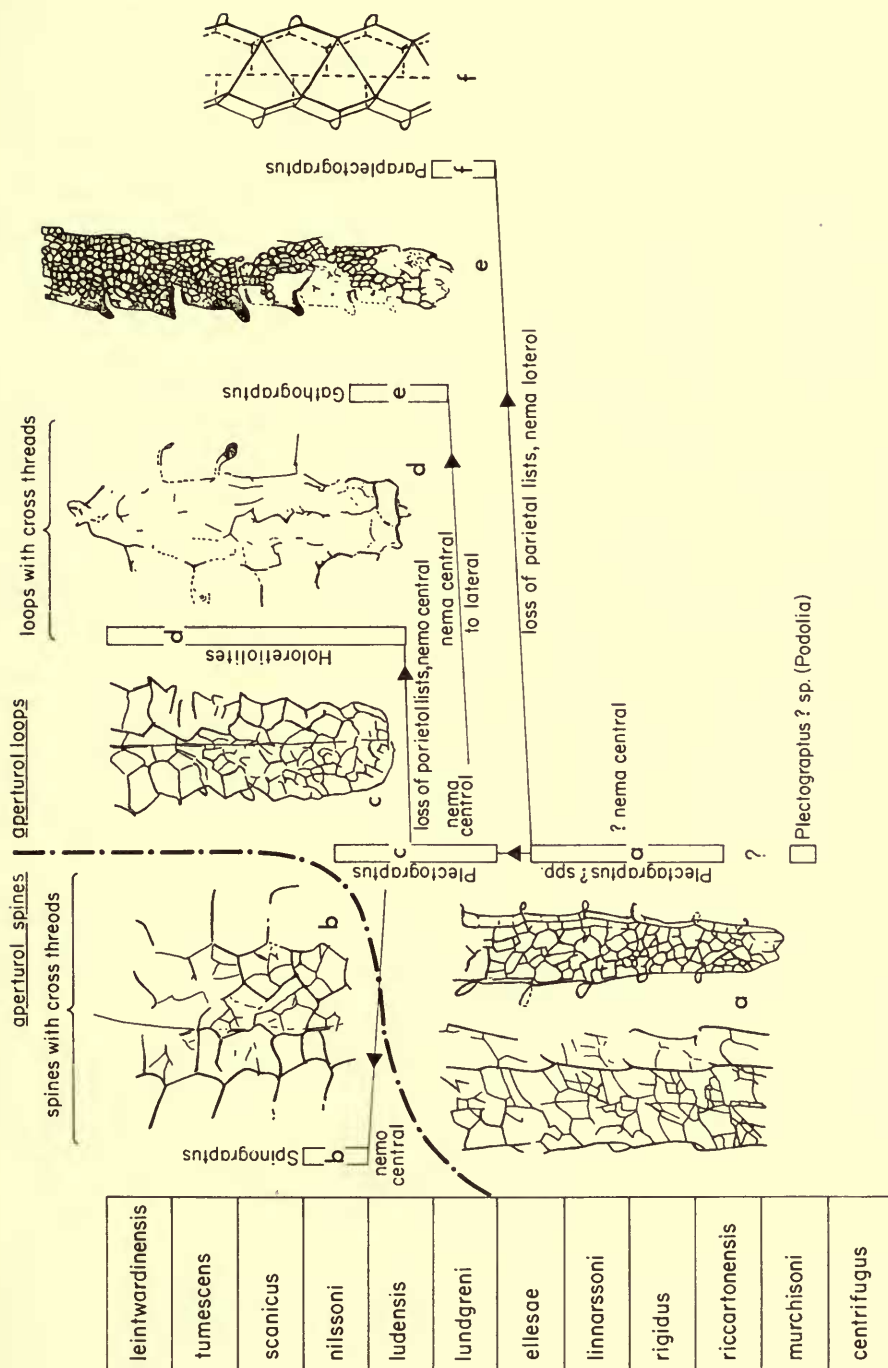


FIG. 16. Evolution of Wenlock and Ludlow retiolitids: a, SM A52624 and SM A52623; b, SM A22495; c, after Bouček & Münch (1952); d, TCD 8473; e, TCD 8653; f, after Bouček & Münch (1952). All figures  $\times 9$ .

then becomes incorporated in a lateral rhabdosomal wall, finally projecting distally from the appendix. The statement by Kirk (1973), that the microfusellar hoods can hardly be genicular since the thecal tube immediately prior to the appendix has one, seems irrelevant: all preceding thecae have a geniculum and a genicular hood, but this carries no implication as to which zooid was responsible for the secretion of them. In fact, the zooid beneath the hood was almost certainly the builder in each case.

It seems likely that *Paraplectograptus* was too specialized to give rise to *Gothograptus*, leaving *Plectograptus* as the only possible source. Any lineage from *Plectograptus* to *Gothograptus* involves the development of a denser reticulum late in the growth of the colony, and the change from a regular subhexagonal clathria to an irregular one with only a suggestion of the zigzag list in some specimens. As in the evolution of *Paraplectograptus*, the parietal lists are probably lost entirely.

*Holoretiolites* has a short nema, central in position, and differs from *Gothograptus* in tapering more rapidly distally and in lacking a reticulum. The thecae are still of climacograptid type, and it may be mentioned that whatever evolutionary lineages are detected in the future, the high Wenlock association of retiolitids with climacograptid thecae (*Plectograptus*, *Gothograptus* and *Holoretiolites*) has evolved through *Plectograptus*? from species of *Retiolites* with more or less orthograptid thecae. *Holoretiolites* may well have evolved from either *Gothograptus* or *Plectograptus*, but the latter is more probable since *Holoretiolites* still has a pronounced zigzag list.

*Spinograptus*, like all these groups, is represented by very few species. The zigzag list is still retained, as are the parietal lists, but the apertures have paired spines (Fig. 16b) directed horizontally and ventrally. The known species have all the appearance of a *Plectograptus* with apertural spines and a fine reticulum, and it is from this genus that the writers feel *Spinograptus* evolved. The nema remains central in position.

In all the above suggestions for evolution within the retiolitids the clathrial elements seem to be the most important in defining the thecal type and in defining changes during evolution. The reticulum appears to be randomly distributed between the genera and species, and presumably represents vacillating attempts at a confining periderm. An interpretation of the nema's position is very difficult, but presumably the sícula in retiolitids is to one side of the rhabdosome, as in *Petalograptus*, and in consequence the nema could be easily incorporated in that lateral rhabdosomal wall, or just as easily left free, as for example in *Archiretiolites*.

#### V. MONOGRAPTINID EVOLUTION

20. The Origin of Monograptids. When Hutt & Rickards (1970) described the evolution of the earliest Llandovery monograptids no monograptid species were known below the *atavus* Zone, where three groups (*atavus*, *cyphus* and *incommodus*) appeared more or less simultaneously. Thus Hutt, Rickards & Berry (1972, abstract only) suggested a possibly diphyletic origin for the monograptids:

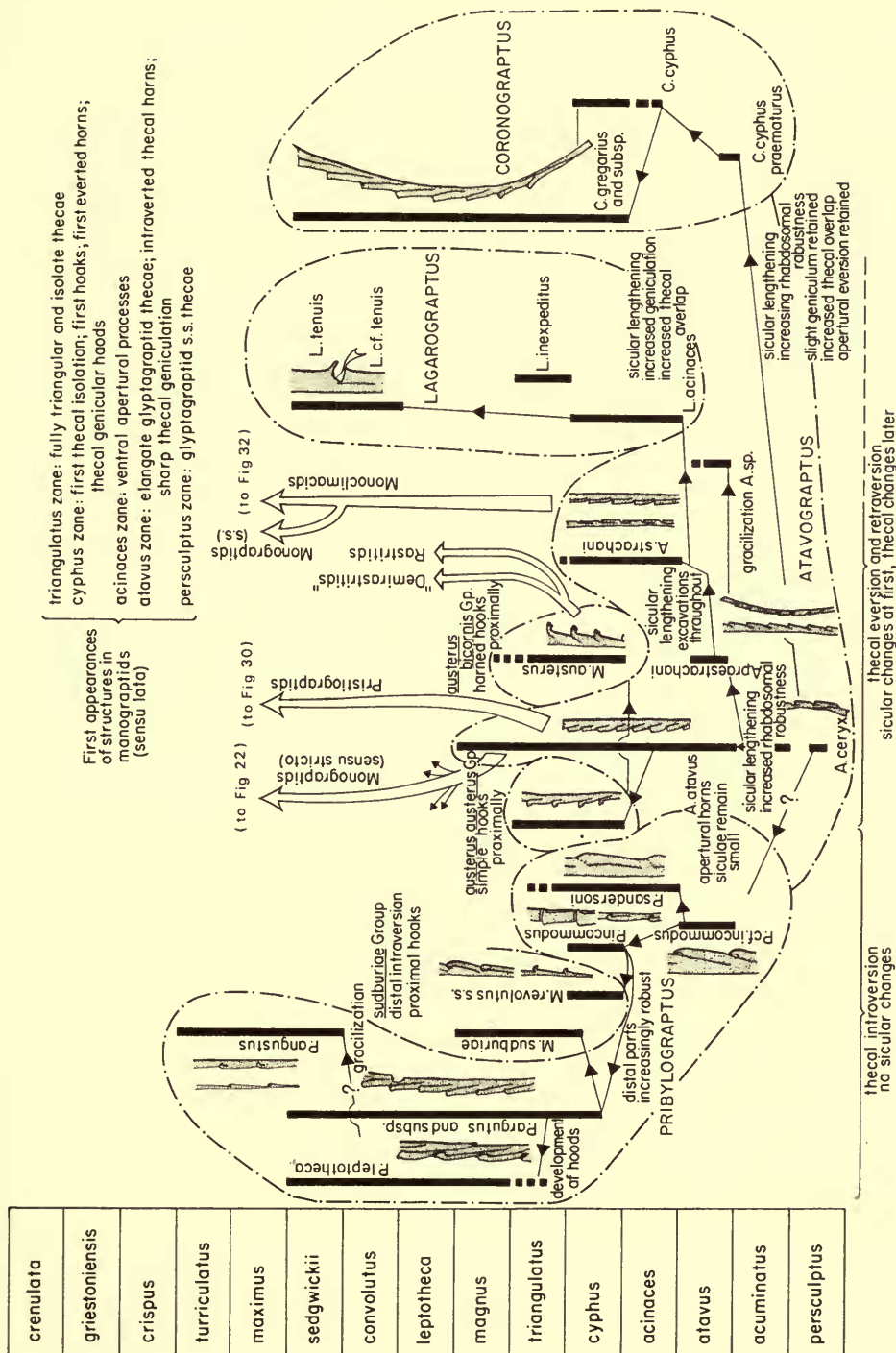


FIG. 17. Evolution of the early monographtids including *Coronograptus*, *Lagarograptus* and *Pribylograptus*. Figures idealized, approximately  $\times 4$ , except *L. tenuis* and *C. cyphus*,  $\times 8$ . *C. cyphus* is drawn for convenience next to the *C. gregarius* and subsp. range rectangle.

the one line involving those species with strongly introverted thecae (the *incommodus* group, or *Pribylograptus* herein; p. 40) and a second with essentially glyptograptid thecae (*atavus* group, *Atavograptus* herein; p. 39; Pl. 4, fig. 4; Pl. 6, fig. 1). Between the Hutt *et al.* (1972) abstract and the actual paper, Rickards (in Rickards & Hutt 1970) discovered a species of *Monograptus* in the *persculptus* Zone of the English Lake District. Hutt has now recorded the same species, *M. ceryx*, in the *acuminatus* Zone on the same section. *Monograptus ceryx* is clearly referable to the *atavus* group, is known in detail from pyritized specimens (Fig. 17) and has undoubted glyptograptid thecae. This last character is so pronounced that if one places a picture of the stipe back to back with its mirror-image, the exact appearance of the biserial *Glyptograptus* is produced (Fig. 18b). It may be emphasized that if this is done with subsequent monograptids the result resembles two monograptids placed back to back, since considerable elongation of the thecal tube has already taken place. Thus the thecal spacing of *Atavograptus ceryx* is 13–15 in 10 mm and that of *A. atavus* may be as low as 5 in 10 mm. It has been pointed out by Dr Valdar Jaanusson (1973) that dithyrial populations might be expected, and we therefore suggest that the form *Glyptograptus* sp. figured by Rickards & Hutt (1970: fig. 2d) might actually be conspecific with *A. ceryx*. The origin of the monograptid uniserial stipe from a biserial ancestor is necessarily a spectacular occurrence: one population was composed of all biserial members, whereas that succeeding may have included some uniserial forms, and the latter population may be considered to exhibit genetic polymorphism. Subsequently the uniserial rhabdosomes would predominate as their ecological advantage was conferred. The nature of this advantage is unknown, but the success of the uniserial rhabdosome from the *atavus* Zone upwards is beyond dispute.

Subsequent to the loss of genetic polymorphism, further changes, in particular the growth of a long, relatively slender, and rather variably flexuous rhabdosome,

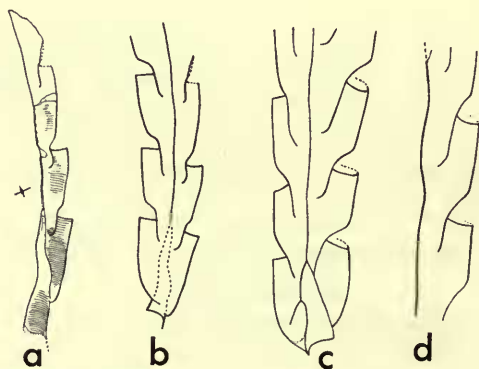


FIG. 18. a, *Atavograptus ceryx* (Rickards & Hutt), SM A67093 (arrows indicate direction of some tectonic compression of the specimen, at right angles to lineation); b, hypothetical biserial constructed by 'doubling up' SM A67093 and by shortening the sicula below the initial bud; c, *Glyptograptus persculptus* s.l., SM A10012; d, half of A10012, idealized, to show basic similarity of thecae to those of *A. ceryx*.  $\times 5$ .



took place at great speed: presumably the uniserial colonies would have had the same energy for growth as their short, stiff, immediate ancestors, and the expected changes would be increased length and, initially at least, lack of stiffness.

The occurrence of an *atavus* group species, *A. ceryx*, in the *persculptus* and *acuminatus* Zones means that once again the possible monophyletic origin of monograptids needs to be considered.

*A. ceryx* could certainly have given rise directly to *A. atavus* by increased length of thecae and sicula. But it is also possible that a second lineage could involve introversion of the thecal apertures, other features remaining much the same. This was suggested by Hutt *et al.* (1972: 171), and N. Sennikov of the Institute of Geology and Geophysics at Novosibirsk informs us that he has obtained a monograptid from the *acuminatus* Zone of the Altai Mountains in which the first three thecae of the rhabdosome are of *ceryx* type but with introverted apertures, and the succeeding thecae of *ceryx* type *sensu stricto*. Such a form may be intermediate between *A. ceryx* and *P. incommodus*, and the lineage involves the proximal introduction of a new feature, namely thecal introversion (Fig. 17). Other aspects of this lineage are discussed below (p. 40).

21. The *atavus* group (*Atavograptus*) and *A. strachani*. The suggested evolution of *Atavograptus* is depicted in Fig. 17, where the range in time, and morphology of the known species, is outlined. The earliest known species, *A. ceryx*, is very reminiscent of *Glyptograptus* in appearance of thecae and thecal spacing, whilst it is possible that the initial bud of the grows fractionally downwards before turning distally (Rickards & Hutt 1970: 118): such a development might be expected if the early populations derived from *Glyptograptus* were dithyrial in nature with both uniserial and biserial members (cf. Rickards & Hutt 1970: 116, figs 2a, d).

*A. ceryx* occurs in the *persculptus* and *acuminatus* Zones and a Russian species possibly intermediate between *A. ceryx* and *P. incommodus* has been found in the *acuminatus* Zone in the Altai Mountains, see above. In the overlying *atavus* Zone the following species of *Atavograptus* have been recorded: *A. atavus*, *Atavograptus* sp. [= *Monograptus* sp. 2 of Hutt & Rickards 1970: 76] (Pl. 4, fig. 5) and *A. praestrachani* sp. nov. [= *Monograptus* sp. 1 of Hutt & Rickards 1970, see p. 102]. These appear at or near the base of the *atavus* Zone.

The suggested lineage from *A. ceryx* to *A. atavus* involves an increase in length of the thecal tubes, including the sicula, and an increase in the length of the rhabdosome. Otherwise the thecae are very alike and the rhabdosomes of generally similar appearance. Other species of less certain stratigraphic and generic position include *M. renaudi* Phillipot. The Russian species, because of the thecal introversion, we suggest should be placed in *Pribylograptus* (Fig. 17; p. 40): the decision is an arbitrary one.

*A. gracilis* and *A. praestrachani* are morphological intermediates between *A. atavus* and *A. strachani* (Hutt & Rickards) which appears in the succeeding *acinaces* Zone. *A. praestrachani* is almost exactly intermediate, having proximal *strachani* thecae and distal *atavus* thecae (Fig. 17), and certainly gave rise to *A. strachani* by proximal introduction and spread of geniculate thecae. The lineage also involves an increase

in the length of the sicula from 2.5 mm in *A. atavus* to 3.0 mm in *A. praestrachani*, and then to over 3.0 mm in *A. strachani*.

*A. strachani*, lacking *atavus* thecae, is included arbitrarily in *Atavograptus* since it is considered slightly closer morphologically to *A. atavus* and *A. praestrachani* than to its suggested descendants (p. 54). Whilst *A. strachani* could not reasonably be placed in *Lagarograptus*, which develops pronounced ventral apertural processes, it could be considered a borderline case for inclusion in *Monoclimacis*, and is in our view a likely forerunner of the early members of that genus (p. 54).

*A. gracilis* probably represents an early tendency towards gracilization in the monograptid stock. Similar tendencies are seen in most groups, particularly in their early stages of evolution: subsequently tendencies to rhabdosomal robustness are more common (e.g. p. 93).

*Atavograptus* is one of the most important genera of Silurian graptolites. It is the first monograptid genus, has relatively simple thecae which provide a good basis for subsequent modifications (geniculation, introversion, thecal hooks), and some of its species (e.g. *A. atavus*) are long-ranging and abundant.

22. *Pribylograptus*. Pribylograptids were the first described monograptids with introverted thecae (Rickards & Rushton 1968). Their discovery led to a greater understanding and unravelling of the complex evolution of the slender early Llandovery monograptids in which the roots of the later important genera are located (Hutt & Rickards 1970, Rickards & Hutt 1970). Hutt & Rickards considered it unlikely that *Pribylograptus* could have given rise to other genera than cladia-bearing types (p. 71), but it has been shown by Hutt (1974) that the paired introverted horns can be modified to extroverted thecal hooks (p. 45), a tendency which affects several stocks in the *cyphus* and *triangulatus* Zones (Fig. 17), and the recognition of which in pribylograptids poses several problems with respect to the origin of hooked monograptids (see below).

The early pribylograptids (Fig. 17; *P. cf. incommodus*, *P. sandersoni*, *P. incommodus*) are very slender species with rather variable flexuous curvature, horned introverted apertures, and with a slight geniculum but lacking a genicular hood. The gentle geniculation reflects their origin from *A. ceryx*: the sicula is only known in *P. argutus* and, as in *A. ceryx*, it is relatively small (1.0 mm). Later pribylograptids (Fig. 17; *P. argutus* and subspecies, *P. leptotheca*) have more robust rhabdosomes and *P. argutus* has a stiff dorsal curvature: both possess genicular hoods. The acquirement of genicular hoods in the span of the *triangulatus* to *sedgwickii* Zones is a feature exhibited by several other groups at the same time (*Lagarograptus*, *Monoclimacis*, as well as biserial species). It is also noteworthy that the development of such complex apertural apparatus in pribylograptids can be contrasted with lack of change displayed by the sicula and the proximal end. In those genera (e.g. *Coronograptus*, p. 41) in which great sicular changes take place, there is little or no modification of the thecae or thecal apertures. Almost all monograptid lineages displayed this feature of considerable development of one or two biocharacters with little or no alteration to the rest.

Following the establishment of *P. incommodus* a tendency to gracilization is probably reflected in the minute species *P. angustus* Rickards from the *sedgwickii* and *turriculatus* Zones: this particular tendency to gracile rhabdosomes is unusual in that *P. angustus* is the last known pribylograptid, although a parallel might be drawn here with the last, small, species of several biserial groups of graptoloids. Earlier forms show the same tendency less spectacularly (*P. argutus sequens* Rickards, *P. jonesi* Rickards) but the main trend within the genus is towards quite robust rhabdosomes.

It is possible that pribylograptids are the ancestors of *Barrandeograptus* (p. 72), and almost certain that the *M. sudburiae* group discovered by Hutt derived from *P. argutus* or a like form. Indeed it is possible that many of the records of *P. argutus* are really referable to *M. sudburiae* since both proximal and distal parts are necessary to identify either. Otherwise the bulk of monograptid groups probably originated from *Atavograptus* and not from *Pribylograptus*.

23. *Coronograptus*. The suggested record and evolution of the coronograptids is shown in Fig. 17. The genus, like *Pribylograptus* and *Lagarograptus* (p. 42), has recently been redefined by Rickards (in press) (see also p. 103) and is taken now to include those species which develop elongation of the sicula (particularly) and thecal tubes, display a slight geniculation, but show little change of the thecal apertures except rare isolation. Increase in the thecal length is accompanied by increased thecal overlap (presumably leading to a lessening of the geniculation) and increased dorsoventral width.

*C. cyphus praematurus* (Toghill) is the earliest recorded species, appearing more or less simultaneously with *A. atavus* in the section at Dobb's Linn. Its origin is certainly within the *atavus* group (its only described uniserial predecessor is *A. ceryx*) and it probably retains, like the other species in the genus, a slight geniculation. The sicula is longer than in *A. ceryx* and the species is best regarded as having originated from the *A. ceryx*-*A. atavus* lineage at or about the base of the *atavus* Zone. The main change is one of increased thecal length and overlap.

*C. c. cyphus*, the succeeding coronograptid, is very similar indeed to *C. c. praematurus* in general rhabdosomal characters but the latter is less tightly curved, in which it is intermediate between *Atavograptus* and *C. c. cyphus*, and has a shorter sicula. *C. gregarius*, including the subspecies *C. g. arcuatus* Obut & Sobolevskaya and *C. g. minisculus* Obut & Sobolevskaya, displays a sicula which increases in length up the stratigraphical sequence to a maximum of 12 mm in specimens of *C. g. gregarius* from the *argenteus* Zone of the Lake District. The *gregarius*-like species, in addition to increased sicula length, exhibit occasional isolation of the thecal apertures but the dorsoventral width does not achieve the proportions of *C. cyphus*.

*Coronograptus* therefore represents a tightly knit low Llandovery genus with unambiguous origins in the *Atavograptus* lineage, and with no traces of subsequent evolution to other genera or groups presumably because of the extreme specialization of the proximal regions. Certainly these species cannot be included in *Pristiograptus* as has been done by some authors (e.g. Strachan 1971): pristiograptids almost certainly originated in certain *magnus*-Zone derivatives of the *atavus* group (p. 64).



24. *Lagarograptus*. Representatives of this genus first appear in the *acinaces* Zone (Fig. 17) in the form of *L. acinaces* (Pl. 6, fig. 3), a species characterized by a delicate *ventral* apertural process, a flowing geniculum, a thecal excavation and a long sicula. Subsequent species, *L. inexpeditus* Obut & Sobolevskaya and *L. tenuis* (Portlock), show little change in the sicula length and position, but the geniculation increases and a pronounced genicular hood is developed above the more semi-circular thecal excavation. The ventral apertural process remains similar, as does the general form of the rhabdosome involving gentle to strong dorsal curvature. It has been shown by Rickards (in press) that the ventral apertural process displays fusellar growth bands, and the presence of such a structure in all the representatives of the genus precludes any obvious connection of it with reproduction (cf. Obut & Sobolevskaya 1968). The genus has been redefined on the bases of the above characters by Rickards (in press), following earlier discoveries by Rickards & Rushton (1968) and Hutt (1968) on the detailed morphology of these and related species groups.

The thecal overlap in *L. acinaces* (Fig. 17) is at least two-thirds, a tendency which affected the *Atavograptus*-*Coronograptus* lineage at about the same time. The overlap apparently lessened in subsequent coronograptids such as *C. gregarius* and the same may have occurred in the later lagarograptids, although the preservation is not always sufficient to be certain. *Lagarograptus* is morphologically the most compact of groups but has a rather long stratigraphical record (Fig. 17) considering its poor representation at each horizon. The origin of *L. acinaces* almost certainly lies with *A. strachani* which had already developed considerable thecal overlap, a geniculum of similar aspect and a long sicula; it has similar rhabdosomal dimensions.

25. The '*revolutus*' group with simple hooks. As a result of Hutt's work on the type *revolutus* specimens of Kurck, the *sudburiae* group of forms with distal introverted thecae was established (p. 45). The remaining '*revolutus*' types fall into two groups, those with simple thecal hooks and those with hooks composed of paired horns. *M. revolutus austerus* Törnquist is the species next in priority after *M. revolutus revolutus* Kurck (now transferred to the *sudburiae* group) and forms a convenient title for the remaining species which are regarded here as subspecies of *M. austerus*. They may be grouped as follows.

1. Forms with simple hooked proximal thecae or possibly with very slight transverse expansion: *M. austerus austerus* Törnquist, *M. austerus* subsp. A (= *M. revolutus* A of Sudbury, *M. a. vulgaris* Hutt 1974), *M. austerus* subsp. D (= *M. revolutus* D of Sudbury, *M. a. sequens* Hutt 1974), *M. difformis* Törnquist.
2. Forms with proximal hooks composed of paired horns: *M. austerus bicornis* Hutt 1974 (= *M. revolutus* B of Sudbury), *M. austerus praecursor* Elles & Wood (i.e. *M. revolutus praecursor* of Elles & Wood) [for *M. revolutus* C of Sudbury, = *M. sudburiae* Hutt, see p. 45].

Those forms in group 2 are discussed in section 26, p. 44. *M. austerus austerus* is the earliest species of the group, appearing in the *cyphus* Zone, possibly a little



earlier than *M. austerus vulgaris* (= subsp. A) and *M. difformis*, both of which occur in the top of the *cyphus* Zone. *M. a. austerus* differs from *M. a. vulgaris* mainly in being less strongly and less regularly dorsally flexed; since Sudbury (1958) has demonstrated that increased dorsal curvature in these forms takes place with time, the distinction may be a real one. Otherwise the two are very similar, with long slender proximal regions comprising at least 25 hooked thecae of low overlap and distal regions with the thecae inclined to the axis at about  $15^\circ$  (Fig. 19).

The only likely ancestors to the *M. austerus* group with simple hooks are in the genus *Atavograptus*. A *Pribylograptus* species close to *P. argutus* almost certainly gave rise to *M. sudburiae* (p. 45), but there is no evidence at all of the considerable changes that would be necessary to derive a form with simple hooks proximally and simple tubes distally from a species with strongly introverted thecae throughout. Therefore we suggest that *M. a. austerus* is derived directly from the earlier

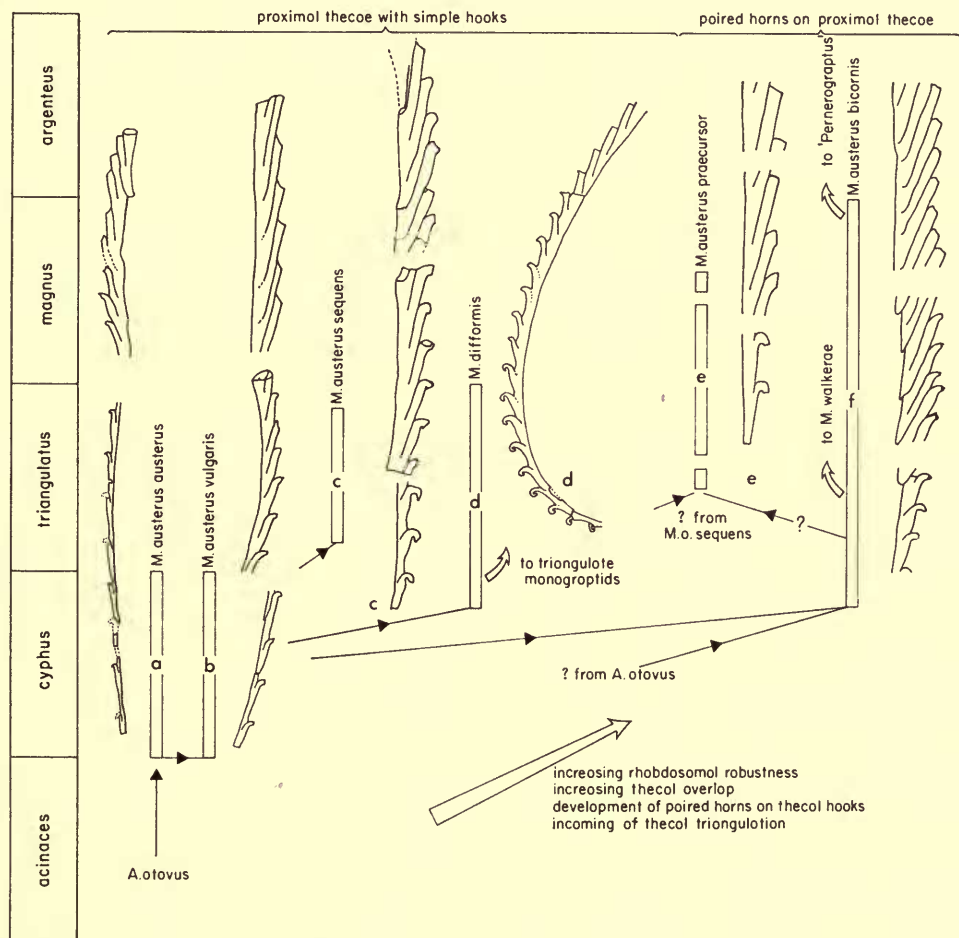


FIG. 19. Evolution of the *M. austerus* group: a, SM A23923; b, GSM Pg1015; c, SM A24508; d, LO 1470T; e, GSM Pg867; f, SM A24505. All figures  $\times 3\frac{1}{2}$ .

*A. atavus*. Unlike later forms of *M. austerus*, with their greater dorsal curvature, *M. a. austerus* has a rhabdosomal form and dimensions similar to *A. atavus*. This resemblance extends even to the nature of the very long slender proximal region of both species. The only changes necessary in such a lineage would be the growth of simple hooks (Fig. 19) on the proximal thecae – proximal introduction of an apertural modification – and a lessening of the *atavus* geniculum particularly in the distal regions of *M. a. austerus*. *A. atavus* itself displays less geniculation in its distal thecae. Therefore *M. a. austerus* is considered a probable direct descendant of *A. atavus*, and a certain direct ancestor of the more stiffly curved *M. austerus vulgaris* (Fig. 19).

*M. a. vulgaris* is followed in the *triangulatus* Zone by *M. a. sequens* (= *M. revolutus* D of Sudbury) which has up to 40 simply hooked thecae, increased thecal overlap (compared with *M. a. vulgaris* where the overlap begins at about th15), an increased dorsoventral and lateral width and increased angle of thecal inclination ( $20^\circ$ ): in short it is a more robust species than *M. a. vulgaris* and has more hooked thecae. *M. a. sequens* is found as high as the top of the *triangulatus* Zone in the Rheidol Gorge (horizon C of Sudbury 1958), and is the highest of the *M. austerus* forms with simple hooked thecae.

*M. difformis* (Fig. 19d) has been shown by Hutt (1974) to appear in the top of the *cyphus* Zone. It is a particularly interesting species in that although clearly belonging to the *austerus* group, it is the earliest species with any triangular thecae. The proximal thecae are axially elongate, the mesial triangular and rather *communis*-like (Fig. 19d) and the distal simple tubes: the change from one type to the next is gradual throughout. The significance of triangular thecae in *M. difformis* is discussed below under sections 28 and 32 (pp. 46 and 52).

26. The '*revolutus*' group with thecal horns. Two forms are known to have proximal thecal hooks composed of paired horns: *M. austerus bicornis* Hutt (= *M. revolutus* B of Sudbury) and *M. a. praecursor* Elles & Wood. The first occurs in the top of the *cyphus* Zone (horizon T of Sudbury 1958) and the second succeeds it in the *triangulatus* Zone. The two are clearly closely related, but *M. a. bicornis* is somewhat more robust with considerably greater thecal overlap and thecal inclination, perhaps suggesting that the two forms originated from a common ancestor by similar processes acting at different rates. Both could have evolved directly from *A. atavus*, a species which extends into the *triangulatus* Zone, but it seems more likely that they have evolved from *M. a. vulgaris* and *M. a. sequens* (Fig. 19) by development of thecal horns from a relatively simple hooked aperture. Interpreted thus it means that apertural horns developed at the top of the *cyphus* Zone in two quite different groups, the *M. sudburiae* group (from *Pribylograptus*; see Fig. 17 and p. 40) and the *M. austerus* group.

This suggested evolution for the *M. austerus* types differs somewhat from that suggested by Sudbury (1958). In the first place it is necessary to exclude her *M. revolutus* C (i.e. *M. sudburiae*) and group it with *M. revolutus* Kurck *sensu stricto* (p. 45). It is far more likely that these evolved from *Pribylograptus* than from *M. a. vulgaris*. Nor is the origin of *M. limatulus* certain, but it is unlikely to have

evolved from a form such as *M. sudburiae* since Hutt (1973) has shown that the tiny proximal thecae have a small, relatively simple hook or hood. This is further discussed on p. 51.

We support Sudbury's (1958) derivation of *M. toernquisti* (= *M. walkerae* nom. nov., see p. 104) from *M. a. bicornis* (= *M. revolutus* B), and the subsequent lineage to *M. pseudoplanus* and *M. planus*. It is of note that the change from *M. pseudoplanus* to *M. planus* through the *convolutus* and *sedgwickii* Zones involves the retreat of the dorsal margin of the thecal aperture and a reduction in the length of the thecal processes (horns to short spines). This is paralleled *at the same time* by the change from *M. sedgwickii* to *M. halli* (p. 49) and the two lineages constitute the only ones which we know of which might be termed regressive. The lineage *M. walkerae* (= *M. toernquisti*) to *M. planus* would, if recent continental practice were followed, require the erection of a new genus to embrace it.

The recognition by two of us (R. B. R. & J. E. H.) that *M. argenteus* has proximal hooks with paired horns suggests that Sudbury's derivation from *M. a. praecursor* may be correct, although she was not aware of paired horns in the latter species and it remains distinctly possible that *M. a. bicornis* is the ancestor of *M. argenteus*. We would derive *M. a. praecursor* from *M. a. bicornis* rather than directly from *M. a. vulgaris*. *M. argenteus* is further discussed on p. 51, and *M. communis* on p. 52.

27. The *sudburiae* group, a new group of biform monograptids. The nature of this group, involving *M. sudburiae* Hutt and *M. revolutus* Kurck *sensu stricto*, has been described by Hutt (1974). It has been shown that the distal thecae in Kurck's type and other material, and in Sudbury's (1958) *M. revolutus* C (= *M. sudburiae*), are strongly *introverted* of the *Pribylograptus* type, that is with paired horns directed dorsolaterally. The proximal thecae in both species have *retroverted hooks*, the change from proximal to distal type involving sympathetic retreat and advance of the dorsal and ventral thecal walls respectively (Fig. 17).

*M. sudburiae* appears in the *cyphus* Zone of the Lake District and extends into the *magnus* Zone, and therefore has a similar range to the other 'revolutus' types (sections 25 and 26 above). Only two alternative origins are possible for the group. Either they acquired the distal introverted thecae by distal introduction of the new character upon a 'revolutus' rhabdosome, or they acquired proximal hooks by proximal introduction upon a *Pribylograptus* rhabdosome. We are strongly in favour of the latter interpretation because the *Pribylograptus* species were already established in the *atavus* Zone, and the tendency to develop 'hooks' (which became strong in the *cyphus* Zone) probably affected *Pribylograptus* just as it affected other groups at the same time. Furthermore, there is no evidence that thecal introversion affected any other groups after its inception through the *Atavograptus*-*Pribylograptus* lineage.

Thus we suggest that *M. revolutus* Kurck *sensu stricto* and *M. sudburiae* Hutt were derived from the *P. incommodus*-*P. argutus* lineage at a point probably close to the origin of *P. argutus* (Fig. 17). At present the group includes only the two species, and although we feel its evolutionary roots to be quite clear and its



evolutionary potential to have probably been low, we would refrain for the present from creating a new genus to embrace the group.

28. '*Demirastrites*'. The status of '*Demirastrites*' has been discussed by Bulman & Rickards (*in* Bulman 1970): it was erected by Eisel (1912) and has *M. triangulatus* as type species, subsequently designated by Bulman (1929). Continental workers have used the concept to embrace those species which in silhouette have *Rastrites*-like thecae at the proximal end and more or less triangular thecae distally (e.g. Přibyl & Münch 1942). That the evolution is extremely complicated, involving many unsuspected morphological features, has been amply demonstrated by Sudbury (1958). Her evolutionary lineages include forms which are not strictly demirastritid (e.g. *M. triangulatus fimbriatus*).

*M. triangulatus* appears at the base of the *triangulatus* Zone slightly before the first rastritids and Sudbury has convincingly demonstrated the origin of *R. longispinus* from *M. triangulatus* through intermediate forms such as *M. t. extremus* following an earlier suggestion of Elles (1922). Other rastritids may have evolved from other 'demirastritid' lineages (e.g. *Rastrites peregrinus*) and the genus is almost certainly polyphyletic.

The origin of *M. triangulatus* (Pl. 5, fig. 3) is problematical, for as well as having triangular thecae it has proximal rastritiform (i.e. *isolate*) thecae. We have shown that thecal isolation may take place in other groups at this time (*Coronograptus*, p. 41, and *Monograptus*, p. 44) whilst triangular thecae are present in *M. difformis* at the top of the *cyphus* Zone. Thus the processes necessary to derive *M. triangulatus* were in operation in late *cyphus*-Zone times. Sudbury did not think *M. revolutus* (= *M. austerus* herein, p. 42) to be a likely ancestor for *M. triangulatus* since the former has a great many axially elongate thecae. However, she did not seem aware of the triangular thecae in *M. difformis*. In our view this feature makes *M. difformis* the only (known) likely ancestor to the *M. triangulatus* group and in particular to *M. t. separatus* (Pl. 2, fig. 2); it should be remembered that the triangulates do have one axially elongate theca, namely *th1*, whilst some have no rastritiform thecae (*M. t. fimbriatus*). Otherwise we strongly support Sudbury's evolutionary suggestions for the triangulate monograptids.

Sudbury suggested four main lineages excepting those known to lead to rastritids. These are: 1, *M. t. fimbriatus* (Pl. 5, fig. 6) to *M. t. similis*, leading eventually to *M. spiralis*; 2, *M. t. major* (Pl. 5, fig. 2) to *M. convolutus* (Pl. 5, fig. 1); 3, *M. t. separatus* to *M. denticulatus*; 4, *M. t. separatus* to *M. decipiens*. The first of these lineages involves the loss of newly acquired rastritiform thecae, and the development of thecal spines from thecal horns (Fig. 20), whilst the second and fourth involve increasing numbers of rastriform thecae and the development of rather long, high triangular thecae. The *M. denticulatus* lineage was presumably regarded by Sudbury as a side branch unlikely to produce further species. Indeed the end products of lineages 3 and 4 above, *M. denticulatus* and *M. decipiens*, are species lacking thecal horns but with relatively simple apertures. It may well be that they had their origins independently in the *M. austerus sequens* lineage mentioned above (p. 44).



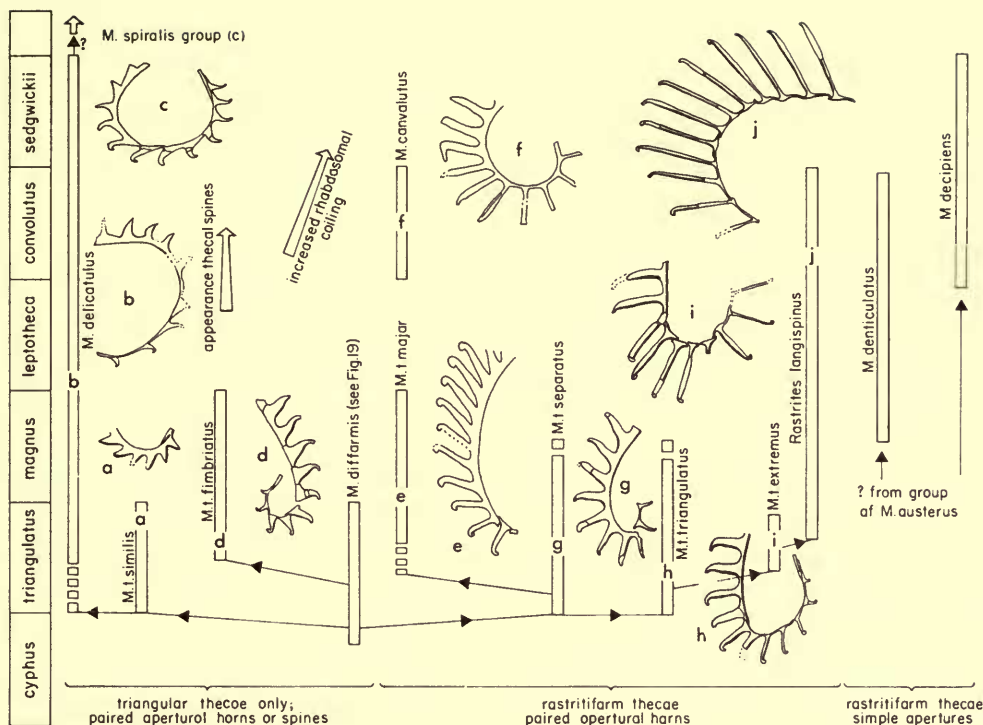


FIG. 20. Evolution of the triangulate monograptids ('*Demirastrites*') and some *Rastrites*: a, SM A21479; b, SM A21431; c, SM A24499; d, SM A24445; e, GSM 26326; f, SM A21293; g, SM A24437; h, SM A24460; i, SM A24479; j, SM A24498. All figures  $\times 3\frac{1}{2}$ .

Thus '*Demirastrites*' could be redefined within the framework outlined by Sudbury (1958), although we do not propose to do this here for two reasons. Firstly, there are too many species (e.g. Přibyl & Münch 1942) the detailed morphology of which is unknown: further study of these might reveal unsuspected complications in lineages proposed on present evidence. Secondly, demirastritids are now known up to and including the *griestoniensis* Zone, yet no successful attempt has been made to unravel their origins, or work out their detailed morphology. On the last point we would tentatively suggest that *M. pragensis pragensis* (Přibyl) (*crispus* Zone) might have evolved from *M. pragensis ruzickai* (Přibyl) (*sedgwickii* Zone).

29. *Rastrites*. The origins of two rastritids, *R. longispinus* (Perner) and *R. peregrinus* (Barrande), have been suggested by Sudbury (1958) to be through *M. t. extremus* and *M. t. praedeciens* respectively. Other rastritids may originate from triangulate monograptids, and Schauer (1967) has outlined some evolutionary lineages within the rastritids themselves.

Schauer distinguishes earlier forms of *R. peregrinus* as *R. p. socialis* which appear closer to the base of the *triangulatus* Zone than does *R. longispinus* in the German

sequence. This does not, of course, obviate Sudbury's suggested origin of *R. peregrinus* from *M. t. praedecipiens*, indeed it tends to give it more weight in that it closes the gap in the record present in the Rheidol section. Presumably *R. p. peregrinus* in the sense of Schauer (*convolutus* Zone) evolved directly from the earlier subspecies, and then gave rise to *R. cf. p. peregrinus* and *R. perfectus* Přibyl. Further, *R. hybridus* and *R. h. gracilis* may have evolved from *R. cf. p. peregrinus* through the morphologically intermediate *R. cf. hybridus*, or possibly from *R. h.* subsp. of Hutt (1975).

Further lineages within the rastritids will have to be worked out following careful studies in different regions of the actual ranges of the species, as well as of their detailed morphology which in many species is but poorly understood. At present it can be stated that following the *R. longispinus* and *R. peregrinus* lineages initiated in the *triangulatus* Zone there are at least two differing groups in the *convolutus* Zone, the *R. approximatus* Perner and the *R. richteri* Perner. The latter has thecae and a rhabdosomal form very similar to *M. denticulatus* (*magnus* to *convolutus* Zones) and may well have evolved from this species. *R. approximatus* Perner, *R. phleoides* Törnquist (*convolutus* Zone) and *R. rastrum* (Richter) (*sedgwickii* Zone) have thecae of the proximal *convolutus* type, even to the presence of pronounced, paired, apertural processes in *R. a. geinitzi* Törnquist and *R. phleoides*: the group may well be related to *M. convolutus*, a 'demirastritid'.

*R. spina*, sensu Schauer (1967), (*sedgwickii* Zone) is of *R. fugax* Barrande type; it may thus form a link with what Schauer terms the *R. linnaei* Barrande group which typifies the lowest parts of the *turriculatus* Zone and which included *R. linnaei*, *R. maximus* Carruthers, *R. carnicus* Seelmeier, *R. distans* and *R. fugax*. *R. spina*, sensu Rickards (1970) and Hutt (1975), is quite different from Schauer's form (Fig. 21) and may well have evolved directly from a monograptid such as *M. sp.* Hutt (Fig. 21) which ranges from the *magnus* at least into the *turriculatus* Zone. *M. sp.* is discussed in more detail on p. 58, but in essence is a *Monograptus* s.s. with isolate proximal thecae and more triangular distal thecae: a 'demirastritid' in the genus *Monograptus*.

Detailed morphological studies may well show that some of the suggested lineages are untenable. In few cases is the nature of the thecal hook in rastritids known. Hutt *et al.* (1970) established that the hook in *R. linnaei* was a rather simplified version of the paired horn triangulate monograptid structure, in which the dorsal margin and the horns themselves had retreated somewhat. Earlier species such as *R. longispinus* have quite pronounced horns, whilst others have extremely long apertural spines perhaps resulting from drawn-out horns (e.g. *R. phleoides*, Fig. 21). It is of great interest that the spinose rastritids reached their acme in the *convolutus* and *sedgwickii* Zones at exactly the same time as spinose 'demirastritids' and spinose monograptids of the *sedgwickii* type and thereafter the dorsal wall of the thecal tube retreated, as it also did in the latter groups.

30. *Monograptus sedgwickii*. Elles (1922) placed *M. sedgwickii* Portlock (Pl. 5, fig. 5) in an intermediate position in a lineage leading from *M. clingani* Carruthers to *M. marri* Perner (Pl. 6, fig. 2) and hence to the *M. priodon* Bronn







ancestor is in the *M. walkerae* (= *M. toernquisti* Sudbury) group. In this group Sudbury (1958) has shown that the slender proximal region with tiny axially elongate thecae is progressively reduced in stratigraphically higher horizons to give rise to species like *M. pseudoplanus* and *M. planus*. This lineage, like the *sedgwickii*-*halli* line, also exhibits retreat of the dorsal margin of the thecal tube and reduction of the horns or spines. Thus the *pseudoplanus*-*planus* line could have evolved *M. sedgwickii* by further, but not complete, straightening of the proximal end and the development of long spines from the paired horns of *M. pseudoplanus*.

31. '*Pernerograptus*'. *M. argenteus* Nicholson is the type species of *Pernerograptus*, a name given by Přibyl (1941) to embrace Elles & Wood's (1901-18) Group IB 1. Bulman (1951) subsequently redescribed the thecae of *M. argenteus* and interpreted them from three-dimensional pyritized specimens as having relatively simple hooks. We have examined many topotypes in three dimensions, and are of the opinion that the thecal hook exhibits the paired horn structures first detected in triangulate monograptids by Sudbury (1958). Thus *M. argenteus* may have evolved from *M. austerus praecursor* as Sudbury suggested, or from *M. a. bicornis* as we suggest. Sudbury was unaware of the paired horn structure exhibited by the thecae of *M. a. praecursor*.

Hutt (1975) has shown that *M. argenteus cygneus* Törnquist is a junior synonym of *M. a. argenteus*, a fact long suspected by some workers (e.g. Rickards 1970), whilst *M. limatulus* Törnquist has tiny proximal thecae with small hood-like hooks quite unlike the horns of *M. argenteus*. The number of species which can be grouped with *M. argenteus* in *Pernerograptus* thus dwindles considerably. The evolutionary relationships suggested above for the *M. austerus* forms with paired horn structures (pp. 42-44) indicate that *M. argenteus* can only reasonably be grouped with *M. a. praecursor* and with *M. a. bicornis*, and that *Pernerograptus* must be restricted to these two species. Some doubts are thus cast upon its utility. Almost certainly future work will show that *M. a. praecursor* and *M. a. bicornis* will have to be raised to specific status to distinguish them from *M. a. austerus* and the simple hook lineage (Fig. 19). We are uncertain of the morphology of *Pernerograptus sidjachenkoi* Obut & Sobolevskaya (1966) from the *convolutus* Zone, and *Pernerograptus omulevkaensis* Obut (1965) from about the *triangulatus* Zone.

---

FIG. 22. Evolution of *M. sedgwickii* and Llandovery and Wenlock *Monograptus* s.s.: *M. sedgwickii* idealized distal thecae,  $\times 9$ ; *M. halli*, Riksmuseum Cn 54941 and Cn 54942,  $\times 9$  and  $\times 4\frac{1}{2}$ ; *Monoclimacis crenularis*, on same slab as BU 1564b,  $\times 13\frac{1}{2}$  approx.; *Monograptus* sp., GSM R56579,  $\times 13\frac{1}{2}$  approx.; *M. marri*, Riksmuseum Cn 54937 and Cn 54938,  $\times 13\frac{1}{2}$  approx.; *Monoclimacis* ? *galaensis*, reconstruction of near proximal thecae, and proximal end with sicula, BU 1569,  $\times 13\frac{1}{2}$  approx.; *Monograptus priodon*, GSM BAH1082,  $\times 3\frac{1}{2}$  approx.; *Monoclimacis griestoniensis*, on same slab as SM A21681,  $\times 22\frac{1}{2}$ ; *M. vomerina vikensis*, SM A62903,  $\times 13\frac{1}{2}$  approx.; *Monograptus firmus*, HUR 40W/1,  $\times 2\frac{1}{4}$ ; *M. radotinensis inclinatus*, HUR 39W/3,  $\times 2\frac{1}{4}$ ; *M. riccartonensis*, BU 1586 and BU 1587,  $\times 2\frac{1}{4}$ ; *M. flexilis*, SM A22317,  $\times 2\frac{1}{4}$ ; *M. flemingii*, BU 1581,  $\times 2\frac{1}{4}$ .

32. '*Campograptus*'. This was established by Obut (1949) with *M. communis* as type species, and originally defined as a dorsally curved monograptid with hooked thecae greatly expanded at their bases. Such a definition is untenable on present knowledge, and it was left to Bulman (1951) and Sudbury (1958) to illustrate the thecal structure. The nature of the thecal hook is known only in the type species (*M. c. communis* Lapworth, *M. c. rostratus* Elles & Wood and *M. c. obtusus* Rickards) where it consists of a relatively simple open hook (Fig. 23) in which both ventral and dorsal thecal walls take part: the lateral part of the apertural lip is slightly convex (Sudbury 1958: pl. 23, fig. 100).

Sudbury suggested an evolutionary lineage of *M. communis* from *M. revolutus praecursor* (= *M. austerus praecursor* herein) and whilst we point out (p. 42) that the latter has paired thecal horns, the superficially similar coeval species *M. austerus* subsp. A (= *M. revolutus* A of Sudbury) has simple hooked thecae; we suggest it as the only likely forerunner of *M. communis*.

Subsequently development of the *M. communis* line involved the loss of two proximal axially elongate thecae to result in *M. c. rostratus* (Sudbury 1958), whilst Rickards (1970) indicated that *M. c. obtusus* from the *sedgwickii* Zone might be a later stage of the same trend in which all the axially elongate thecae had been lost. Should then *M. millipeda* (*argenteus* Zone) and *M. clingani* (*convolutus* Zone) be referred to *Campograptus*? They have no axially elongate thecae but are uniform monograptids with a basic *communis*-like thecal tube. The hooked part of the metatheca in *M. millipeda* occupies a much greater proportion of the thecal tube than in *M. communis*, whilst the aperture itself faces the dorsal side of the rhabdosome. That is, the larger hook is more enrolled than in *M. communis* (Fig. 23). However, the hook itself seems to be of simple type and there is a suggestion of slight convexity of the lateral apertural walls as in *M. communis*.

*M. millipeda* is perhaps best regarded as an offshoot from the *M. communis* lineage in which the processes leading to *M. c. rostratus* have taken place more fully. Considered thus *M. c. obtusus* could have evolved either from *M. c. communis* or from *M. millipeda*. The former seems a more likely ancestor since the hook in *M. millipeda* is already much more tightly enrolled than in the later *M. c. obtusus*. In any event *M. millipeda* seems a likely candidate for a redefined *Campograptus*.

*M. clingani* (Pl. 4, fig. 3) should probably also be included in a redefined *Campograptus*, although the nature of the thecal hook is less certain than in *M. millipeda* and general rhabdosomal form is as a rule little better than a rough guide (p. 86). We are uncertain of the position in this scheme of *C. elegans* Koren', whilst *C. curtus* Obut & Sobolevskaya (in Obut, Sobolevskaya & Merkuryeva 1968) has been placed in synonymy with *M. millipeda* by Hutt (1975).

It has been suggested above (p. 49) that *Rastrites richteri* might well have evolved from *M. denticulatus* by loss of the mesial and distal thecal type. A further point about *M. denticulatus* is that the distal thecae resemble the thecae of *M. millipeda* which occurs in the preceding zone. The tendency to produce rastritiform proximal ends at these levels applied to *M. millipeda* or *M. communis* would certainly result in a form very close to *M. denticulatus* (Fig. 23). Hutt (1975), however, has recently recorded *M. denticulatus* from the *magnus* Zone. The possibility of a single lineage

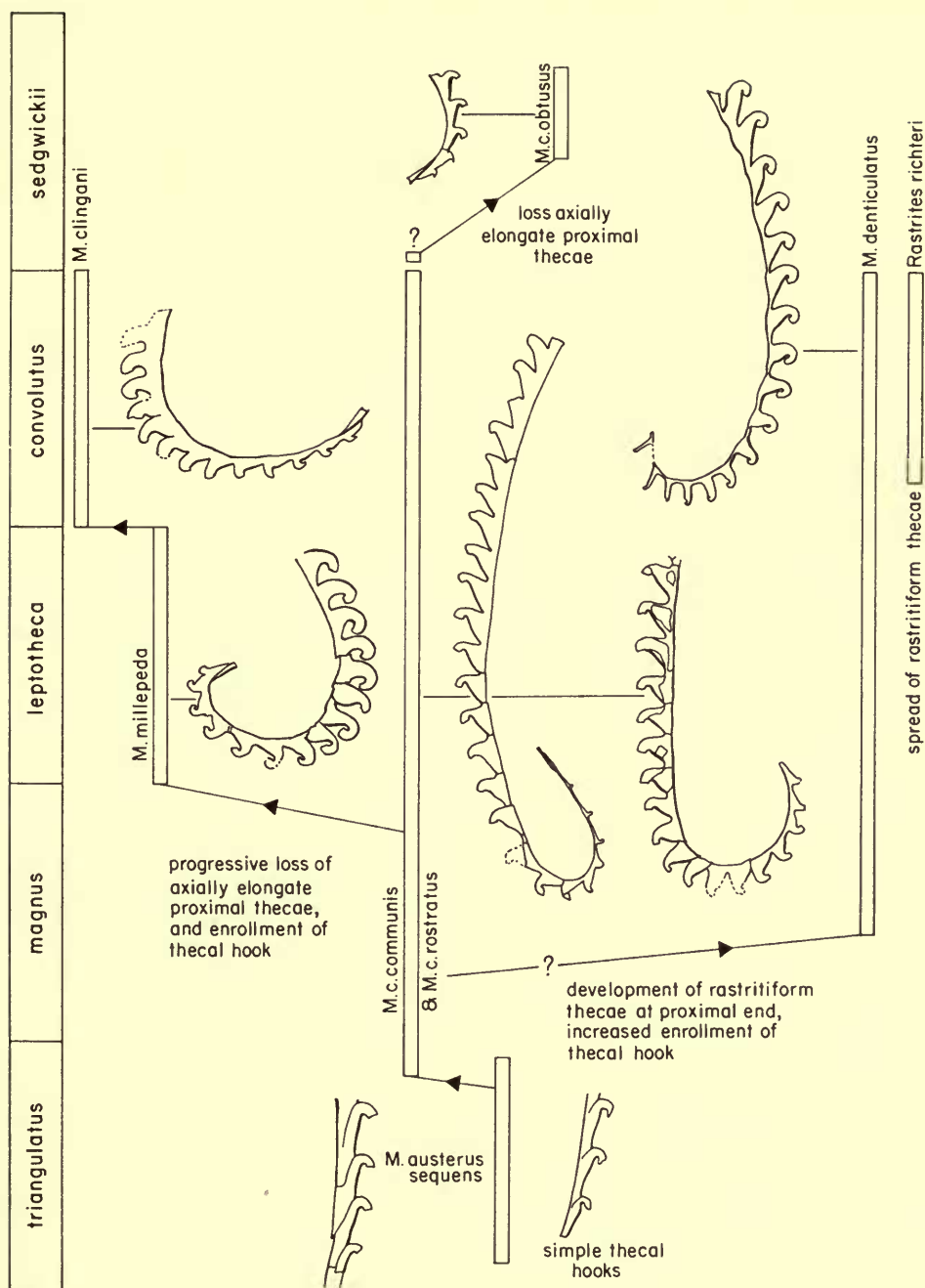


FIG. 23. Evolution of the *M. communis* group ('Campograptus'): *M. austerus sequens*, SM A24508; *M. c. communis* and *M. c. rostratus*, respectively SM A24487 and SM A24493; *M. denticulatus*, SM A21418a; *M. millepeda*, LU 57684; *M. clingani*, LU 57688; *M. communis obtusus*, HUR S80,8.4/90. All figures  $\times 4\frac{1}{2}$ .



evolving from '*Pernerograptus*' *austerus sequens*, to '*Campograptus*' *communis*, to '*Campograptus*' ? *millipeda*, to '*Demirastrites*' *denticulatus*, to *Rastrites richteri* (Fig. 23) emphasizes our disquiet about this system of generic classification which blindly ignores the problems of polyphyletic relationships, and is one of the reasons for our reluctance to accept the usefulness of '*Campograptus*' among others.

33. *Monoclimacis* is one of the more important upper Llandovery to low Wenlock genera, but its roots are undoubtedly in the middle to low Llandovery. Preceding the certain monoclimacids, such as *M. griestoniensis*, *M. crenulata* (Pl. 6, fig. 4) and *M. vomerina* at the top of the Llandovery, are the relatively less common species *M. ? galaensis* Lapworth (*turriculatus* and *crispus* Zones) and *M. crenularis* Lapworth (*convolutus* Zone). Both species have been re-examined by Rickards (1968), who interpreted the former as basically a monoclimacid but with paired, lateral lappets at the apertures. The lappets are more elongate on the proximal thecae, and in profile often look like simple hooks. Specimens of *M. crenularis* are usually less well preserved, but the thecae have a pronounced geniculum, more or less vertical supragenicular walls, and the proximal thecae at least have some form of 'hook'. The 'hook' may consist of a combination of apertural eversion and a genicular hood. Quite well preserved pyritized specimens have recently been collected from the Lake District (Hutt 1975) and whilst these show the monoclimacid thecal tube and geniculum quite clearly, the nature of the 'hook' itself remains somewhat obscure. The distal thecae on this material undoubtedly possess a genicular hood.

A monoclimacid close to *M. crenularis* has recently been obtained from the *argenteus* Zone of the Lake District (Hutt 1975). This form differs from *M. crenularis* in being rather more slender and in having more widely spaced thecae, but the proximal thecae are 'hooked' and distal thecae have a clear geniculum, genicular hood and vertical supragenicular wall. The species is quite close in rhabdosomal dimensions, shape, thecal spacing and structure of thecae (excluding 'hooks' and hoods) to *Atavograptus strachani* Hutt & Rickards (1970), which occurs in the *acinaces*, *cyphus*, and possibly *triangulatus* Zones. We therefore propose the following lineage leading to *Monoclimacis crenularis* - *A. praestrachani*, to *A. strachani*, to *Monoclimacis* sp., to *M. crenularis*. The evidence is that *M. crenularis* Lapworth and its immediate ancestor should be regarded as true monoclimacids.

Subsequent evolution within *Monoclimacis*, prior to the *vomerina* group, is difficult to unravel partly because the basic thecal form of *M. ? galaensis* closely resembles that of the *Monograptus marri*-*M. priodon* lineage, and partly because the record of monoclimacids prior to the *griestoniensis* Zone is so poor. The possible link with *Monograptus* s.s. is discussed further below, p. 60. There are probably undescribed monoclimacids in pre-*griestoniensis* Zone strata, and a few have been described and left under open nomenclature (e.g. *M. ?* sp. A of Rickards 1970).

From the *griestoniensis* Zone upwards to the middle Wenlock monoclimacids are well represented by numerous species which fall naturally into two groups, a slender one based upon *M. griestoniensis* and a robust upon the type species of the genus, *M. vomerina*. The detailed evolution of the whole plexus is being studied at



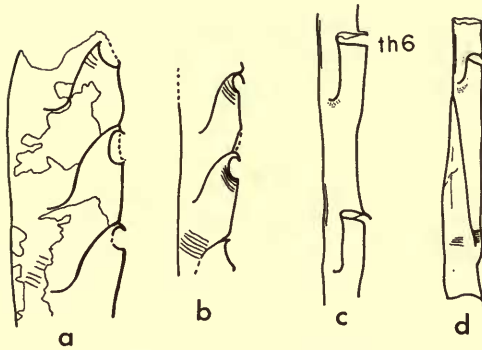


FIG. 24. a, b, *Monoclimacis* of *vomerina* group, GSM PW226, proximal and distal portions of same specimen showing pronounced thecal apertural eversion beneath a genicular hood,  $\times 12\frac{1}{2}$ ; c, d, *M. griestoniensis*, on same slab as SM A21681, the specimen figured by Elles & Wood (1901-18: text-fig. 279b),  $\times 25$ .

present by one of us (R. B. R.), but it can be said that the main difficulty with monoclimacids has been in working out their morphology. Rickards & Smyth (1968) concluded that the genicular hood in *M. flumendosae* (Gortani) was composed of microfusellar tissue, and this has been confirmed from isolated material. But it is distinctly possible (Fig. 24) that the hood in other species consists of excessive growth of the dorsal thecal wall relative to that of the ventral wall. In many, if not most, monoclimacid species the thecal apertures are strongly everted and are almost always overhung by a genicular hood of some kind, particularly in the proximal thecae. The genicular hood of the proximal thecae may be so strongly developed that in profile it may have almost the appearance of a *priodon*-like hood. This fact coupled with the generally similar prothecal proportions and thecal overlap occasionally makes the distinction between *Monograptus* s.s. and *Monoclimacis* s.s. quite difficult.

Urbanek (1958) described *Monoclimacis micropoma* (Jaekel) from the Ludlow, and was the first, in fact, to elucidate the microfusellar hood structure in monograptids (first detected in *Gothograptus nassa* by Holm 1890). In the *lundgreni* Zone of the Wenlock only one monoclimacid is known (*M. flumendosae*) and this differs from all the earlier species in having a flowing geniculum and not quite vertical supragenicular wall. The general form of this species is so unlike *M. micropoma* that it seems unlikely that it has given rise to the latter, and the possibility exists that Ludlow monoclimacids have arisen independently. Mihailova (personal communication) has presumably reached this conclusion in designating some Ludlow species as *Pseudomonoclimacis*. It is exceedingly difficult to make a morphological distinction between Ludlow monoclimacids and those from the Llandovery and Wenlock, or to suggest potential ancestors other than the Ludlow save-all genus *Pristiograptus*. When the range in variation in thecal form in *P. haupti*, which includes some development of a geniculum in the thecae in some specimens (Urbanek 1958), is considered, it might be regarded as a possible ancestor.

34. *Monograptus* s.s. (including *Mediograptus*). A theoretical derivation of *Monograptus* s.s. is easily achieved by spread of the simple hooked thecae of the *M. austerus* group throughout the length of the rhabdosome, but until recently there were very few likely contenders at the right horizons of *triangulatus* to *convolutus* Zones. Prior to the *magnus* Zone no forms referable to *Monograptus* s.s. have been recorded.

The earliest form of which we are aware is a specimen collected by Dr H. Jaeger in 1966 from the Dobb's Linn section at about the level of the *magnus* Zone (top of the *gregarius* Zone as defined by Toghill 1968b: *D. magnus* has since been recorded from the same horizon). This is illustrated in Fig. 25 as *Monograptus* s.s. sp. A. The 67 mm long specimen has hooked thecae throughout the length of the rhabdosome, but otherwise resembles the *M. austerus* group species in all features of rhabdosome size, shape, thecal spacing and basic structure of the prothecal tube. The thecal hooks are seen to be constructed by excessive growth of the dorsal margin relative to the ventral wall, and the ventral lip of the theca is clearly visible beneath the retroverted dorsal wall. Fusellar structure has been detected on the hooks, which do not retreat on the distal thecae. There is little or no sign of transverse expansion. The hook, therefore, differs from the later *priodon* type in that the ventral thecal wall takes no part in it. If, hypothetically, the retroverted dorsal wall were removed from the distal thecae, the remaining rhabdosome would closely resemble *M. austerus*. If all the hooks were removed it would be close to *A. atavus* except that the sicula is too small.

The next similar species of which the authors are aware is *M. undulatus* Elles & Wood (*convolutus* Zone). This has closely similar rhabdosome shape, size and thecal dimensions, and like *Monograptus* sp. A may have thecal overlap of up to one-third. Elles & Wood (1901-18) noted the similarity of the proximal end to that of *M. sedgwickii*, and *M. undulatus* is certainly a possible ancestor of that

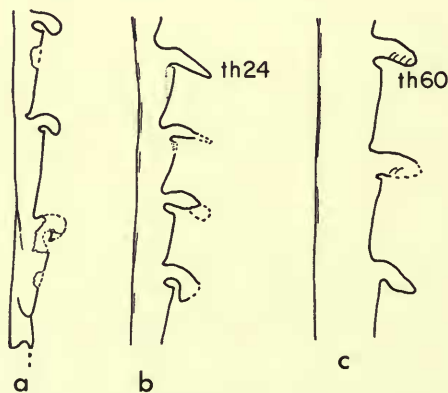


FIG. 25. a-c, *Monograptus* sp. A, proximal, mesial and distal thecae of same specimen, SM A89948,  $\times 25$ , showing basic *atavus*-like appearance but with strong hooks and hoods composed of fusellar tissue: hypothetical removal of these hoods results in a form very similar to *A. atavus*. Horizon is top of *gregarius* Zone, Dobb's Linn.

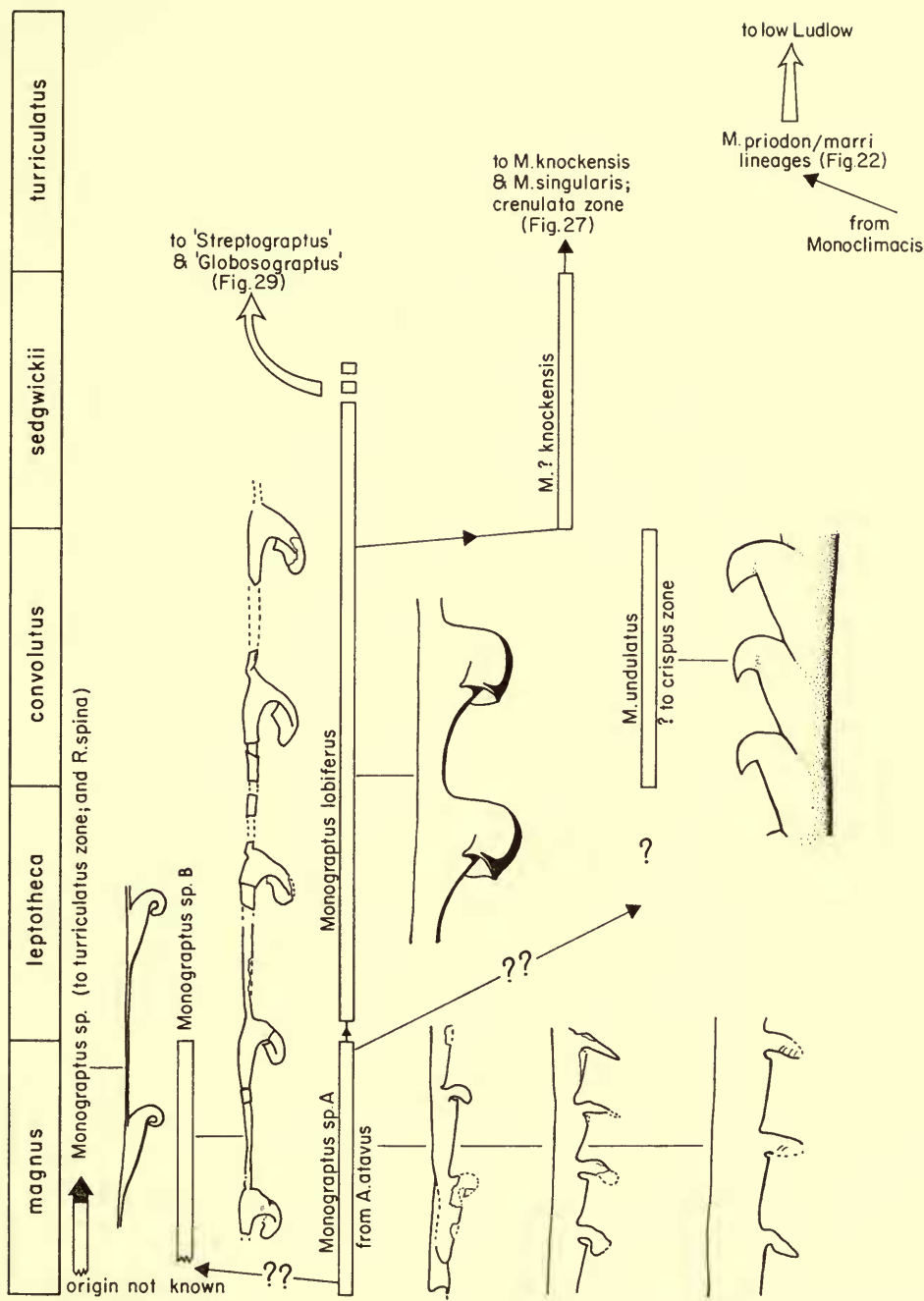


FIG. 26. Evolution of lobate monograptids: *Monograptus* sp. A. as in Fig. 25 (opposite); *Monograptus* sp. with enrolled metathecae, LU 57782; *Monograptus* sp. with isolated metathecae, HUR S73.9.4/79; *M. lobiferus*, idealized after Bulman (1970); *M. undulatus*, GSM 26309. All figures  $\times 22\frac{1}{2}$ .

species. However, we prefer to suggest a derivation of *M. sedgwickii* from a triangulate monograptid, thus obviating the need to reduce thecal overlap to nil without change of rhabdosome shape to help the process. The thecal hook in *M. undulatus* appears to involve mostly growth of the dorsal thecal wall.

It might be thought, therefore, that at this level in the Llandovery the potential existed for derivation of, say, the *M. lobiferus* types and the *M. priodon* types. But the position has been complicated by the discovery in the *magnus* Zone of the Lake District of the lobate species *Monograptus* sp. B (Fig. 26) and of *M. sp.* Hutt (Fig. 26). Both are uniform monograptids, the former resembling later derivatives of the *M. lobiferus* group and the latter being unique in its isolation of apparently *Monograptus* s.s. hooks. Thus there are three apparently unrelated *Monograptus* species already present in the *magnus* Zone but as yet no records below this level. All three are slender species and it is quite possible that there are undescribed, slender, uniform *Monograptus* species with thecal hooks in the *triangulatus* Zone.

*M. sp.* is a species possibly derived from the triangulate monograptids, or from the *M. austerus*-*M. communis* lineage, by isolation of the proximal type of axially elongate thecae. In view of the simple *priodon*-like hooks, that is with both dorsal and ventral thecal walls participating and lack of thecal horns, the second possibility seems more likely. The axially elongate thecae of *M. communis* are not unlike the distal thecae of *M. sp.*, which certainly suggest that thecal isolation is a proximally introduced character as it is in all other known cases.

*Monograptus* sp. B (Fig. 26) is a very early example of what is commonly achieved at higher horizons in the *lobiferus* group (below), in that both ventral and dorsal thecal walls form a pronounced hook, and then at least the dorsal wall turns proximally and finally dorsally, resulting in a dorsally-facing tube closely adpressed to the ventrally-facing early metatheca. The origin of this form must remain in great doubt, the best that can be said being that it is an early offshoot from the *M. sp. A*-*M. lobiferus* lineage.

There can be little doubt that the lineage *Monograptus* sp. A (*magnus* Zone) to *M. undulatus* (*convolutus* Zone) led to *M. lobiferus* M'Coy (Pl. 5, fig. 4), probably as early as the *argenteus* Zone or at the latest by the base of the *convolutus* Zone. It is possible that the Rickards (1970) records of *M. lobiferus* from the *argenteus* Zone should be referred to *M. millipeda*. *M. lobiferus* differs from *M. undulatus* in being a more robust graptolite in which the lobed effect created by excessive growth of the dorsal thecal wall has become more marked (Fig. 26). It is now known that *M. lobiferus* also has apertural tube-like processes developed from the dorsolateral margins of the aperture (Fig. 27) and directed lateroventrally. Such a structure poses some problems for the apparently obvious sequence of successors to *M. lobiferus*, namely *Monograptus* ? *knockensis* Rickards (1970), *M. knockensis* Elles & Wood and *M. singularis* Manck. As has been pointed out above, the problematical *M. sp. B* is the earliest known case of thecal lobation, but the trend towards acquiring thecal lobes of some kind in several groups really began at about the level of the *sedgwickii* Zone with *M. ? knockensis* (*sensu* Rickards 1970). This trend was followed shortly after by the acquisition of prothecal folds in different groups.



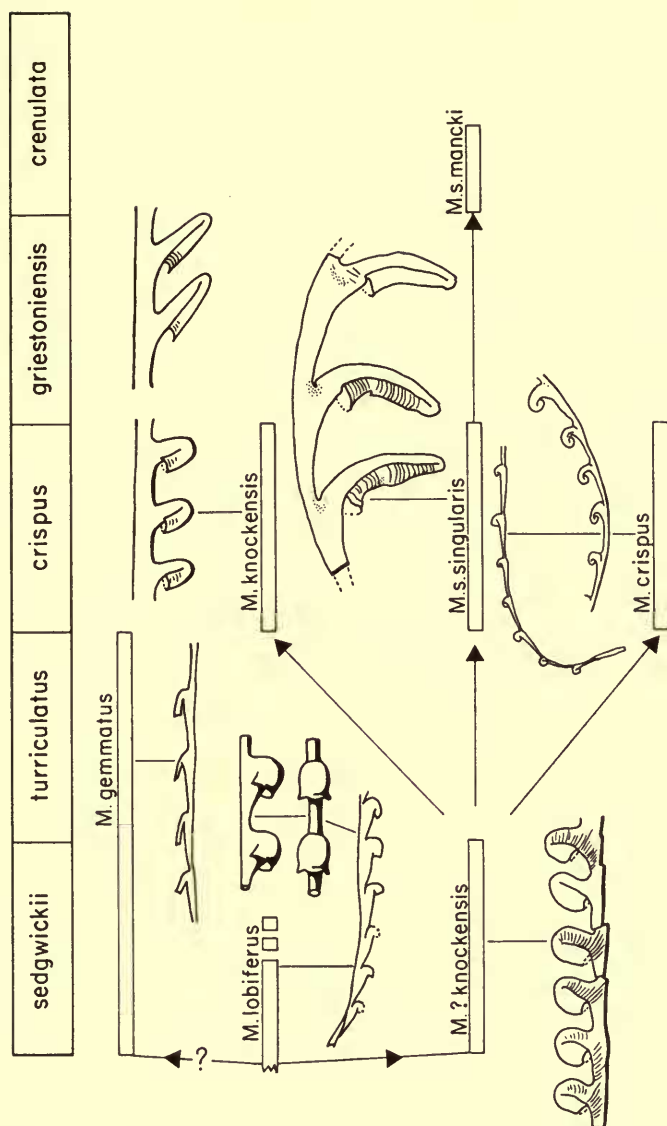


FIG. 27. Evolution of *knockensis* group of lobate monograptids: *M. lobiferus*, idealized after Bulman (1970) and LU 57720,  $\times 12\frac{1}{2}$ ; *M. gemmatus*, HUR S94.5.4/40,  $\times 5$ ; *M. ? knockensis*, HUR S80.8.4/144,  $\times 5$ ; *M. knockensis*, SM A21974, proximal and distal thecae,  $\times 5$ ; *M. singularis*, LO 10131T,  $\times 12\frac{1}{2}$ ; *M. crispus*, BU 1650 and Belfast Natural History Museum figured Elles & Wood (1909-18: text-fig. 314b),  $\times 5$ .

The possible links of the *lobiferus*, *knockensis* and *priodon* lines of evolution with such 'genera' as *Globosograptus*, *Streptograptus* and *Mediograptus* is discussed below, but it is necessary first to examine the possible origins of the *priodon* line of evolution which becomes increasingly important from the *turriculatus* Zone upwards into the Wenlock.

*M. marri* Perner (Pl. 6, fig. 2), commonly regarded as the immediate ancestor of *M. priodon* (e.g. Elles 1922) first appears in the upper third of the *turriculatus* Zone, that is well above the *R. maximus* Subzone and the *M. halli* horizons. The thecal structure has been recently described from isolated material by Hutt *et al.* (1970), where it is seen that as in *M. lobiferus* the hook has a pair of ventro-laterally directed open tube-like processes. However, the thecal hook is not lobed in the extreme manner of *M. lobiferus* and the ventral thecal wall also takes part in the hook (Fig. 22). Therefore if *M. marri* evolved from *M. lobiferus*, ignoring for the moment the unbridged gap of at least the *maximus* Subzone, it would have to be by a pronounced retreat of the dorsal wall of the thecal tube, coupled with advance of the ventral wall. The process does occur, partially, in other groups (e.g. the *sedgwickii-halli* line) at this time, but it would have to be reversed in the later *marri-priodon* development.

There is, however, a more satisfactory alternative origin for *M. marri*, namely from the *Monoclimacis* stock, the *crenularis-galaensis* line. Unlike *M. lobiferus* this line has rhabdosomes of exactly the same size and shape as *M. marri* but lacking the thecal hooks. Instead they have genicular hoods and paired lappets. The simple process of coalescence of these lappets dorsally would produce a *priodon*-like thecal hook. The coalescence of lappets to produce hooks has already been detected in the astogeny of *Cyrtograptus* and, indeed, may yet be proved in *M. galaensis* or *M. crenularis*. Further, the hook of *M. marri* displays two features which *Cyrtograptus rigidus* thecal hooks also show, namely a median indentation of the dorsal lip where coalescence takes place along the zigzag line, and ventro-laterally directed tube-like processes. The latter do not occur in *C. rigidus* on the thecae immediately following the hooked ones. Thus the suggested origin of *M. marri* is depicted in Fig. 22 where it will be noted, additionally, that there are no stratigraphical problems with which to contend. Following the split giving rise to the *priodon*-line both *Monograptus* s.s. and *Monoclimacis* expanded into numerous species. *M. marri* extends up to the *crispus* and possibly *griestoniensis* Zones where it becomes difficult to distinguish the two species *M. marri* and *M. priodon*. It seems certain that the latter evolved from *M. marri* by the formation of a longer thecal hook with an entire dorsal lip, and by increased robustness of the rhabdosome as a whole. Whilst more slender forms were evolved at times (e.g. *M. parapriodon* Bouček) the essential evolution was to the Wenlock robust forms of *M. priodon* and later to the robust and spinose *M. flemingii*. Offshoots from the main line almost certainly produced various species such as *M. firmus* Bouček, *M. radotinensis* Bouček, *M. riccartonensis* Lapworth etc. each of which has various biocharacters developed at the expense of others. Various collections of *M. riccartonensis* show that extreme variants have pronounced dorsal flexure, in contrast to the usual gentle flexure, and it is almost certain that there is a progression through *M. flexilis belophorus* to *M. flexilis flexilis* in which the dorsal curvature is both pronounced and characteristic. The suggested lineage involves an increase in the metathecal proportions from the beak-like hook of *M. riccartonensis*.

One difficult problem in this interpretation has been the recent recognition of extremely robust spinose *priodon*-types in the *turriculatus* Zone. Bassett &

Rickards (1971) described *Monograptus* sp. A from the *turriculatus* Zone of Cross Fell, northern England, the Southern Uplands and from Norway. This was later described by Hutt (1975), with additional evidence from the Lake District (Fig. 22). The species bears a striking resemblance to the middle and upper Wenlock *M. flemingii* (Salter) and can only be interpreted, whatever its origin, as having achieved the *flemingii* condition at an extremely early stage in the evolution of the group. In this respect it parallels the lobate *M.* sp. B from the *magnus* Zone, and as has been suggested earlier in this account, innovation often seems to occur firstly with great rapidity to be followed by a less successful (morphologically speaking) attempt to achieve the same thing. The rapid innovation is, in effect, 'before its time' and usually characterizes a short side line of evolution. *M.* sp. A of Bassett & Rickards almost certainly belongs in this category.

*Mediograptus* Bouček & Přibyl (in Přibyl 1948) is said to differ from *Globosograptus* and *Streptograptus* by the 'less coiled ends of the thecae'. *Streptograptus* is discussed below (p. 67), but it has been shown that some forms usually placed in *Streptograptus* (*M. antennularius* Meneghini) have exactly the same thecal hooks as others placed in *Mediograptus* (*M. minimus cautleyensis* Rickards; Bulman & Rickards in Bulman 1970; Fig. 28). In both these species the dorsal and ventral walls participate in what is virtually a *prionon*-type hook except that the ventrolateral processes typical of the latter are reduced to rather rounded wing-like processes. It is certain that other *Mediograptus* and *Streptograptus* species have the same structure, that the thecae are not 'coiled' in any way, and that they are best regarded

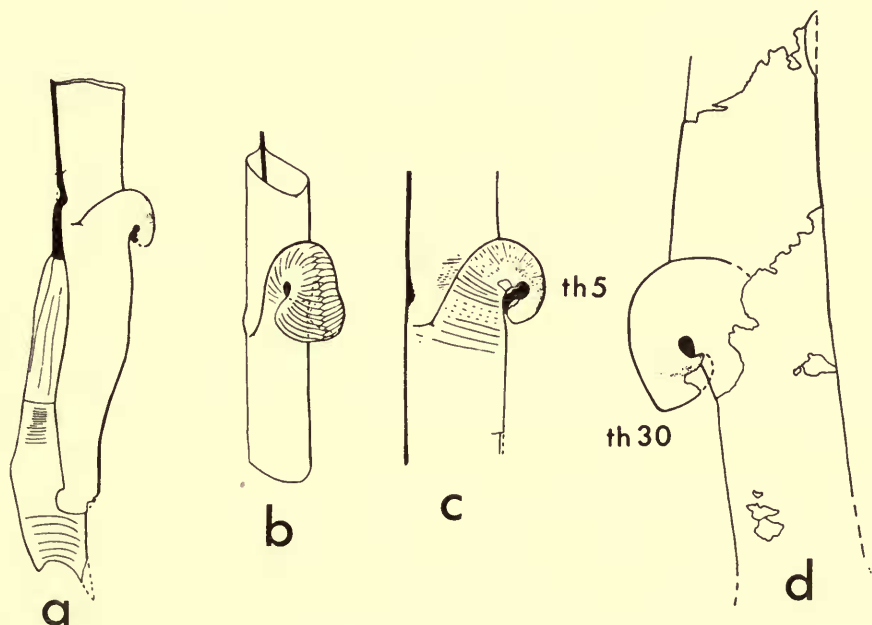


FIG. 28. a-c, '*Mediograptus* *minimus cautleyensis*'; d, '*Streptograptus* *antennularius*'; after Bulman & Rickards (in Bulman 1970).  $\times 50$ .

as *Monograptus sensu stricto* which have evolved from either the main *priodon* lineage or the *lobiferus* lineage by acquiring slight rhabdosomal changes (Fig. 29). The rhabdosomes may be almost straight, dorsally or ventrally curved, or both. As in other groups with more slender species (e.g. *Oktavites*, p. 73) rhabdosomal curvature seems of little classificatory value.

The structure of *Globosograptus* species is less certain, but the distal thecae, whilst still axially elongated in the manner of the proximal ones, are higher with a supposed 'enrolled' late metathecal portion. The nature of the hook has not yet been determined and the affinity of the few species sometimes placed here, as well as the value of the 'genus' itself, is very doubtful.

Another problematical morphological feature of some *Monograptus* species is the recently-discovered prothecal fold. Prothecal folds have been discerned in some species previously regarded as mediograptids but which are here considered somewhat simplified offshoots from *Monograptus* (Fig. 29); they are also known in *Oktavites* (p. 73) and in streptograptids (Figs 29, 32) and, again, may reflect a trend affecting several different lineages at more or less the same time, namely from near the base of the *turriculatus* Zone upwards.

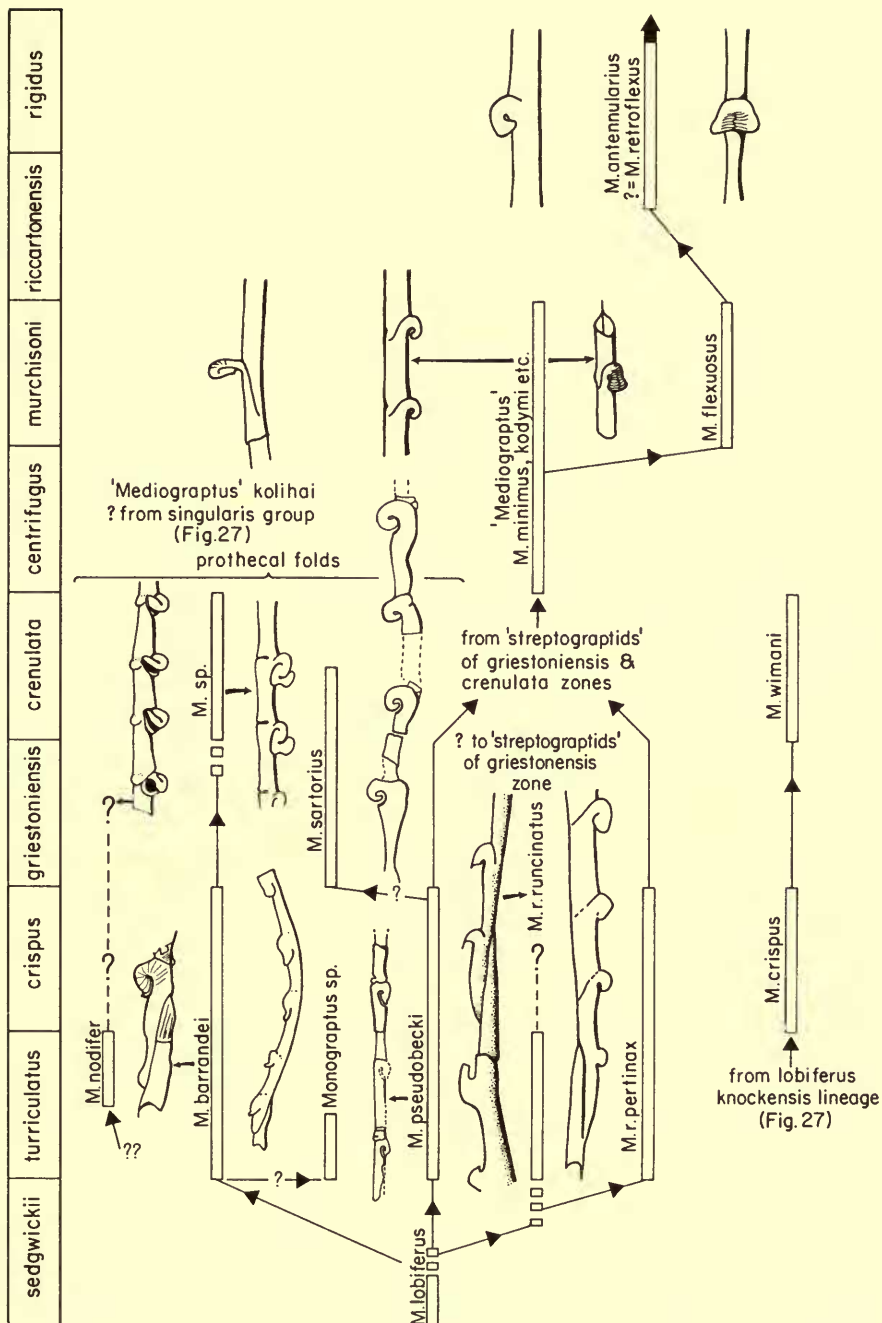
From the above it will be clear that we consider *Monograptus sensu stricto* to be polyphyletic. Whilst there may be some clarity around the *priodon*, *undulatus* and *lobiferus* lineages this does not extend to include evolution within '*Mediograptus*', '*Globosograptus*' and '*Streptograptus*'. The last occurrences of *Monograptus sensu stricto* are in the low Ludlow in the form of such species as *M. unguiferus* Perner and *M. uncinatus* Tullberg. One of us (R. B. R.) has isolated specimens of *M. unguiferus* (SM A64520-4) in beds yielding *M. colonus compactus* Wood and *P. dubius* (Suess), and these, like Urbanek's (1958) specimens of *M. uncinatus*, are striking in their resemblance to low Wenlock specimens of *M. priodon*. Unlike the late Ludlow and early Devonian hooked monograptids, *M. unguiferus* and *M. uncinatus* are undoubtedly related to the earlier *priodon-flemingii* lineage although the poor record of them in the *ludensis* Zone remains a problem (see section II above, p. 10). Nevertheless this relatively small gap in the record hardly compares with that between the *nilssoni-scenicus* Zones and the *fecundus* Zone where links between the *priodon* and *hercynicus* lines are lacking.

35. *Pristiograptus*. Reference to Fig. 1 (p. 7) will indicate the highly important nature of this genus in the evolution of the Silurian graptolites: from it stems the last known evolutionary burst of graptoloids. Like *Monoclimacis* the early evolution

---

FIG. 29. Evolution of '*Streptograptus*', '*Mediograptus*' and other lobate monograptids: *M. pseudobecki*, TCD 8638,  $\times 11\frac{1}{2}$ ; *M. r. runcinatus*, Lapworth Collection, after Strachan (1952),  $\times 11\frac{1}{2}$ ; *M. r. pertinax*, LU 57728,  $\times 11\frac{1}{2}$ ; *Monograptus* sp., LU 57715,  $\times 11\frac{1}{2}$ ; *M. barrandei*, Riksmuseum Cn 54924,  $\times 13\frac{1}{2}$  approx.; *M. nodifer*, LO 1041t,  $\times 9$  approx.; *Monograptus* sp. showing superficial resemblance to *M. nodifer* but with excessive growth of the dorsal, as opposed to ventral, margin of the thecae,  $\times 9$  approx.; *M. sartorius*, LO 1032t,  $\times 11\frac{1}{2}$ ; '*Mediograptus*' *kolihi*, after Rickards & Iordan (1975),  $\times 11\frac{1}{2}$ ; '*Mediograptus*' *minimus*, after Bulman & Rickards (in Bulman 1970),  $\times 13\frac{1}{2}$  approx.; *M. antennularius*, after Bulman & Rickards (in Bulman 1970),  $\times 9$  approx.





was rather slow, and its roots have previously been considered obscured in the great plexus of low to middle Llandovery evolution. The earliest robust pristiograptid of which we are aware is *P. concinnus* (Lapworth) which occurs in the *argenteus* Zone in the Howgill Fells (Rickards 1970) and Lake District, and also as low as the *triangulatus* Zone in the Lake District and Rheidol Gorge. The species is very close to *A. atavus*, retaining a slight geniculation reflected mainly in the gently convex free ventral wall, and in fact is morphologically and stratigraphically intermediate between *A. atavus* and *P. regularis* (Fig. 30; Pl. 5, fig. 7). The last species has lost all traces of the geniculum but retains the long slender rhabdosome of the earlier forms and the relatively small early thecae and sicula. The lineage also exhibits a gradual reduction in the length of the sicula compared with its *atavus* ancestors.

The only other early *Pristiograptus* species are *M. fragilis fragilis* Rickards (*cyphus*–*convolutus* Zones), *M. f.* subsp. Hutt (*acinaces* and *cyphus* Zones) and two undescribed forms from the *magnus* Zone of the Lake District (Figs 30, 55). *P. fragilis* probably reflects a tendency to gracilization on the part of the *A. atavus* stock: geniculation had already been lost and the thecae are long, quite simple tubes. Once again these forms are best regarded as an early successful production of the pristiograptid morphology, to be followed by a slower, less spectacular repeat of the same process in the *atavus*–*concinnus*–*regularis* lines. The two undescribed forms (Figs 55a, b) are clearly of this latter lineage, and may actually be morphological intermediates between *P. concinnus* and *P. regularis*, just as they are stratigraphical intermediates.

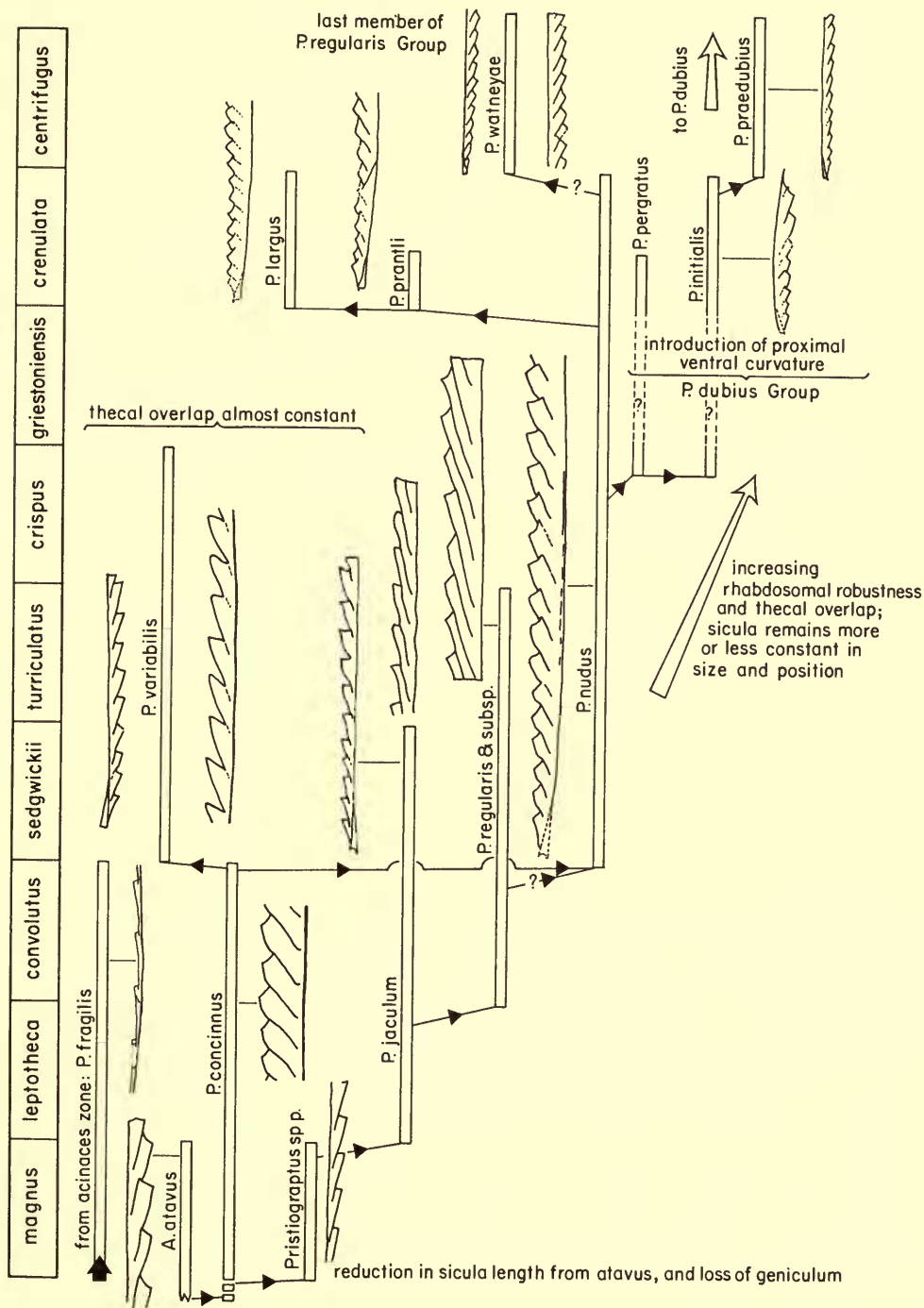
Thus the *regularis* line was established quite low in the Llandovery. It persists into the basal Wenlock where it is represented by one species (*P. watneyae* Rickards). In order of appearance in the record the *regularis* line is represented by the following species:

1. *P. concinnus* (*triangulatus*–*sedgwickii* Zones)
2. *P. jaculum* (*argenteus*–*sedgwickii* Zones)
3. *P. regularis* (*convolutus*–*turriculatus* Zones)
4. *P. variabilis* (*turriculatus*–*crispus* Zones)
5. *P. nudus* (*turriculatus*–*crenulata* Zones)
6. *P. watneyae* (*centrifugus* Zone)

All these species, and their subspecies, have very long rhabdosomes, occasionally up to 200 mm, and slender, straight proximal regions with small siculae. *P. nudus* (Lapworth) (Pl. 2, fig. 5) is the first species to deviate from the group pattern in that the proximal end is rather more robust and occasionally with slight ventral curvature

---

FIG. 30. Evolution of the Llandovery *Pristiograptus* species: *P. fragilis*, LU 57587,  $\times 4\frac{1}{2}$ ; *P. concinnus*, after LU 57564,  $\times 4\frac{1}{2}$ ; *P. sp.* after LU 57772,  $\times 4\frac{1}{2}$ ; *P. jaculum*, after Elles & Wood (1901–18: text-fig. 244a) and BU 1459,  $\times 4\frac{1}{2}$ ; *P. variabilis*, SM A21634 and SM A21635,  $\times 4\frac{1}{2}$ ; *P. regularis*, SM A20956,  $\times 4\frac{1}{2}$ ; *P. nudus*, HUR 5Wi/6,  $\times 4\frac{1}{2}$ ; *P. largus*, after Přibyl (1945),  $\times 2\frac{1}{4}$ ; *P. pranlii*, after Přibyl (1945),  $\times 2\frac{1}{4}$ ; *P. watneyae*, HUR 37W/17,  $\times 2\frac{1}{4}$ ; *P. initialis*, after Přibyl (1945),  $\times 2\frac{1}{4}$ ; *P. cf. praedubius*, SM A52621,  $\times 2\frac{1}{4}$ .



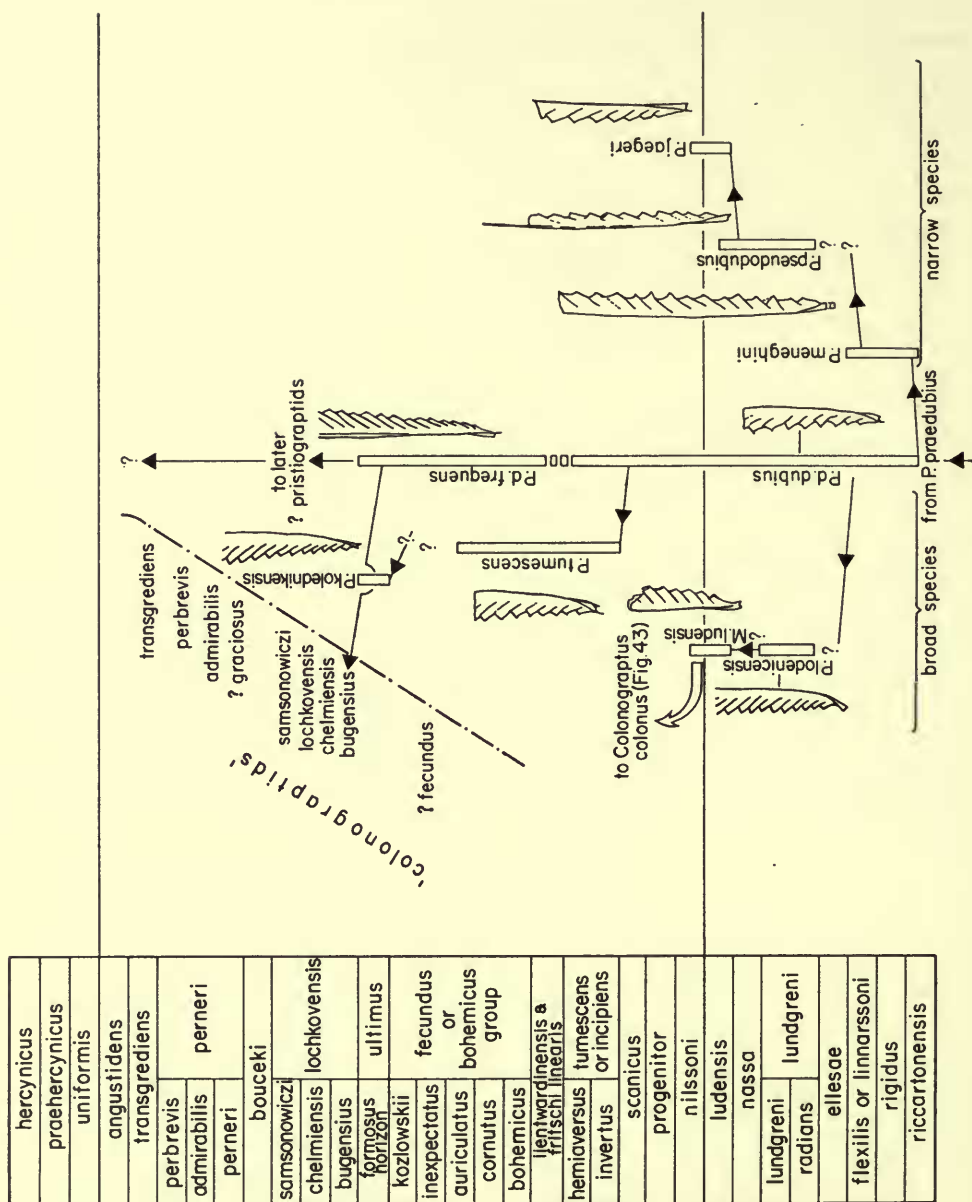


FIG. 31. Evolution of Wenlock and later *Pristiograptus* species: *P. dubius*, BU 1463; *P. meneghini*, HUR 17N/46; *P. pseudodubius*, HUR 26N/11; *P. jaegeri*, TCD 8661; *P. lodenicensis*, after Přibyl (1945); '*Monograptus*' *ludensis*, SM A60900; *P. tumescens*, BU 1472; *P. dubius frequens*, after Přibyl (1945); *P. kolednicensis*, after Přibyl (1945). All figures  $\times 2\frac{1}{2}$ .



(Fig. 30). *P. denemarkae*, *P. pergratus* and *P. initialis* (*crenulata* Zone) almost certainly evolved from *P. nudus* (Fig. 30) and this line led to the low Wenlock *P. praedubius* and hence to the critically important *P. dubius* lineage which then persisted into the Pridoli. The *regularis* lineage is essentially Llandovery, and the *dubius* lineage essentially Wenlock upwards, but the two overlap briefly in the *crenulata* to *centrifugus* Zones.

Through the Wenlock *P. dubius* repeatedly produced short-lived broad and narrow species and subspecies: *P. dubius latus* Bouček, *P. pseudolatus* Rickards, *P. meneghini* (Gortani) and *P. pseudodubius* (Bouček). The tendency was continued less spectacularly in the Ludlow (e.g. *P. d. ludlowensis* Bouček, *P. frequens* Jaekel and *P. vicinus* Perner), but more importantly the *P. dubius* lineage provided the basic stock for many genera by spectacular modifications of the simple, tubular, pristiograptid aperture (*Colonograptus* etc.). These modifications are dealt with in the appropriate sections below (42 onwards, pp. 77–82).

36. '*Streptograptus*'. A large number of species were placed in Yin's (1937) genus by Bouček & Přibyl (1943) but the type species, *M. nodifer* Törnquist, is at present unique in its thecal structure (Fig. 32). Other species commonly placed



FIG. 32. *Monograptus nodifer* Törnquist, LO 1041t,  $\times 20$ , showing the unique thecae of the type species of '*Streptograptus*'; the ventral flange may be formed by excessive growth of the ventral thecal wall; probably *turriculatus* Zone.

here (*M. antennularius*, *M. exiguus* Nicholson) we include in other genera on the evidence provided by detailed morphological studies (pp. 63, 73). But the structure of a majority of the species included in *Streptograptus* by Bouček & Přibyl is unknown, although it can be confidently predicted that some will turn out to have the *Monograptus* s.s. thecae of *M. antennularius*: if and when this is established it may be possible to elucidate the evolution of the *antennularius* types.

Hutt *et al.* (1970) described a species as *M. cf. barrandei sensu* Elles & Wood in which the thecae exhibit prothecal folds and a strongly retroverted or lobed dorsal thecal wall with little or no growth of the ventral thecal wall (Fig. 29). The apertural region of the dorsal wall has an upturned median lip. The horizon is low in the *turriculatus* Zone of Dalarne, Sweden. It is possible that this thecal type is ancestral to the more complex *nodifer* type which is typical of higher horizons (? *turriculatus* to *crenulata* Zones). *M. sp.* Hutt (*turriculatus* Zone) is a possible intermediate in that it has attained the *nodifer* fish-hook rhabdosome but still has the *barrandei* hook and upturned lip. Excessive growth of this lip, to the extent that it finally resulted in the aperture facing the dorsal margin, would lead to *M. nodifer* s.s. (Fig. 29).

*M. nodifer* was recorded from the *turriculatus* and *crispus* Zones by Elles & Wood (1901-18) but it is far from certain from their figured specimens whether these



FIG. 33. *Monoclimacis cf. griestoniensis* (Nicol), Oslo Museum 39550,  $\times 12\frac{1}{2}$ , a bipolar siculate rhabdosome; high Llandovery.

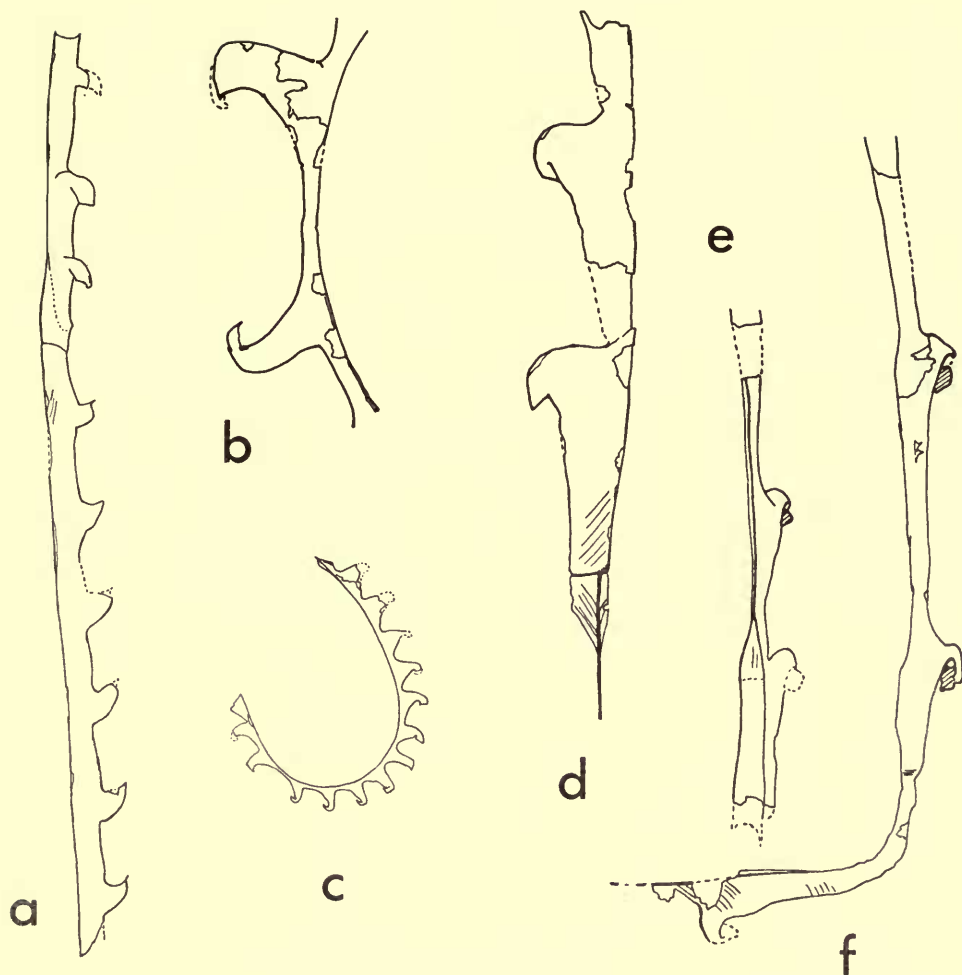


FIG. 34. Comparison of siculate bipolar rhabdosome (a) with regenerative bipolar rhabdosomes: a, *Monograptus sedgwickii*, GSM CV7645,  $\times 12\frac{1}{2}$ , *sedgwickii* Zone; b, c, *M. cf. decipiens*, GSM NIC5076/7,  $\times 12\frac{1}{2}$  and  $\times 2\frac{1}{2}$  respectively, *convolutus* Zone; d, early regenerative growth of *M. lobiferus*, SM A81836,  $\times 12\frac{1}{2}$ , *convolutus* Zone; e, f, siculate specimen and regenerative specimen of *M. aff. sartorius*, LO temporary no. 111,  $\times 12\frac{1}{2}$ .

really are Törnquist's species. On the other hand, Hutt (1975) has recorded *M. nodifer*? from the *turriculatus* Zone of the Lake District, so that the *nodifer* hook may appear as early as this zone.

Finally we would mention species such as *M. runcinatus* Lapworth, sometimes placed in *Diversograptus*, in which the hook (considered a lobe by Bouček & Přibyl 1943) seems not unlike the *undulatus* type. Some similar species, whether with prothecal folds or not, are probably best considered in *Monograptus* s.s. and not as streptograptids, the usual practice.

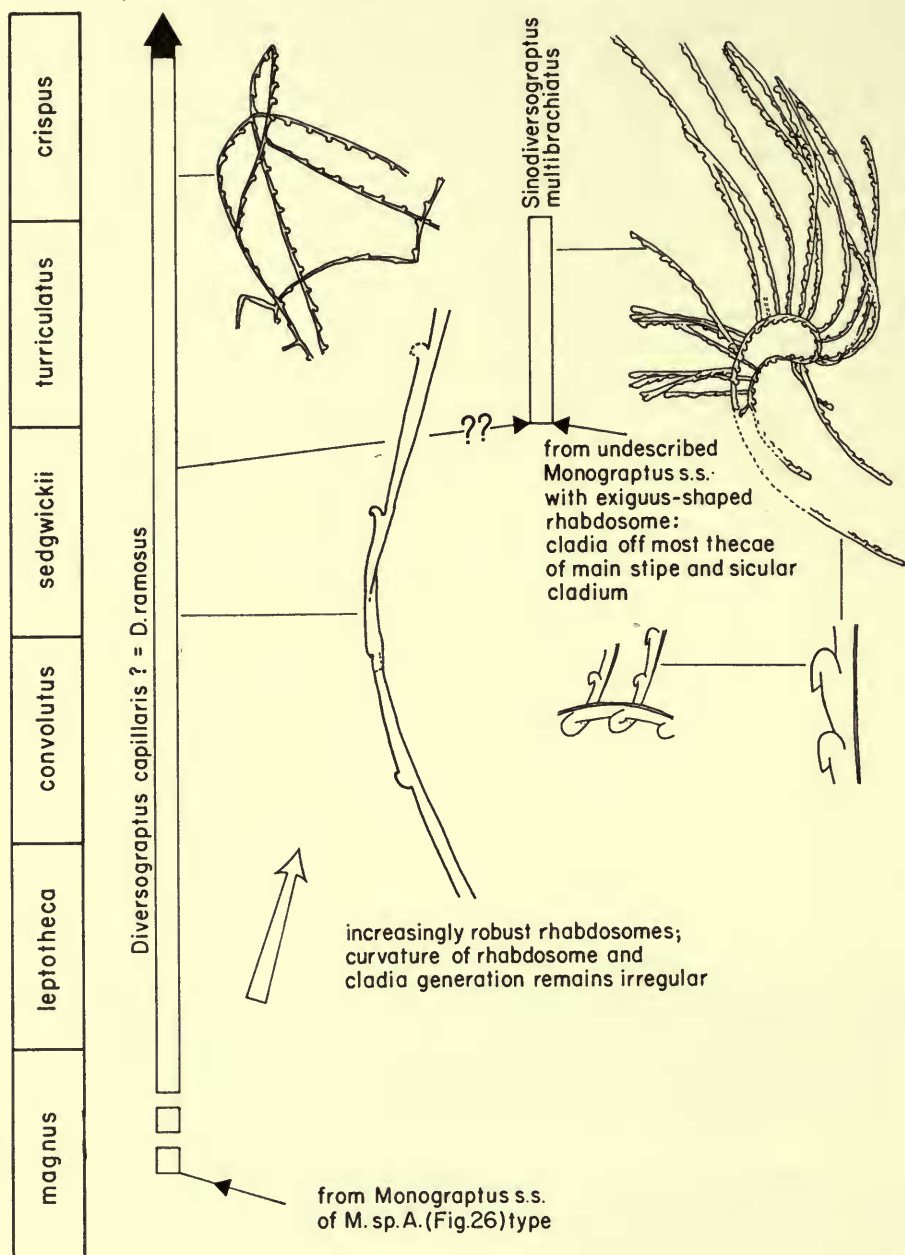


FIG. 35. Evolution of *Diversograptus* and *Sinodiversograptus*: *D. ramosus*, proximal end  $\times 35$  approx., Royal Institute of Natural Sciences, Belgium, IG11.077; cladia-bearing portion of rhabdosome,  $\times 2$ , after Bouček & Přibyl (1954); *Sinodiversograptus multibrachiatus*,  $\times 1\frac{1}{2}$ ,  $\times 5$  and  $\times 10$  respectively, after Mu & Chen (1962); specimen no. 11580a.



37. *Diversograptus*, *Sinodiversograptus* and *Barrandeograptus*. The genus *Diversograptus* Manck has recently been revised by Rickards (1973) who demonstrated that sicular cladia were present on the type specimens, and were also found in quite unrelated groups, such as in *Monoclimacis* cf. *griestoniensis* Nicol (Fig. 33). The diversiform procladium condition, as opposed to bipolar rhabdosomes resulting from regeneration of broken stipes (Fig. 34), is a late astogenetic growth stage potentially achievable in most monograptid groups although it has not yet been established in any members of the *prionon* lineage. Regeneration of broken stipes is similarly to be found in a number of groups including triangulate monograptids (Fig. 34) and is no criterion for inclusion in the genus *Diversograptus*.

*Diversograptus* and *Sinodiversograptus* are probably of some value as genera at present since both the main stipe and sicular cladium generate at least secondary cladia. In *Diversograptus* these are widely spaced and irregular in distribution, even uncommon, but in *Sinodiversograptus* they are developed from most of the main stipe thecae and sicular cladial thecae. The hooks in both genera are of the *undulatus* or *lobiferus* type, that is not enrolled tightly, and it is certain that they evolved from *Monograptus* s.s. not from *Streptograptus* as commonly supposed. One of us (R. B. R.) has been fortunate enough to examine good specimens of *Sinodiversograptus* from Tienshan, and, like the figures of the Chinese specimens, these exhibit an *undulatus* type of hook (Fig. 35). The main stipe is of *exiguus*-

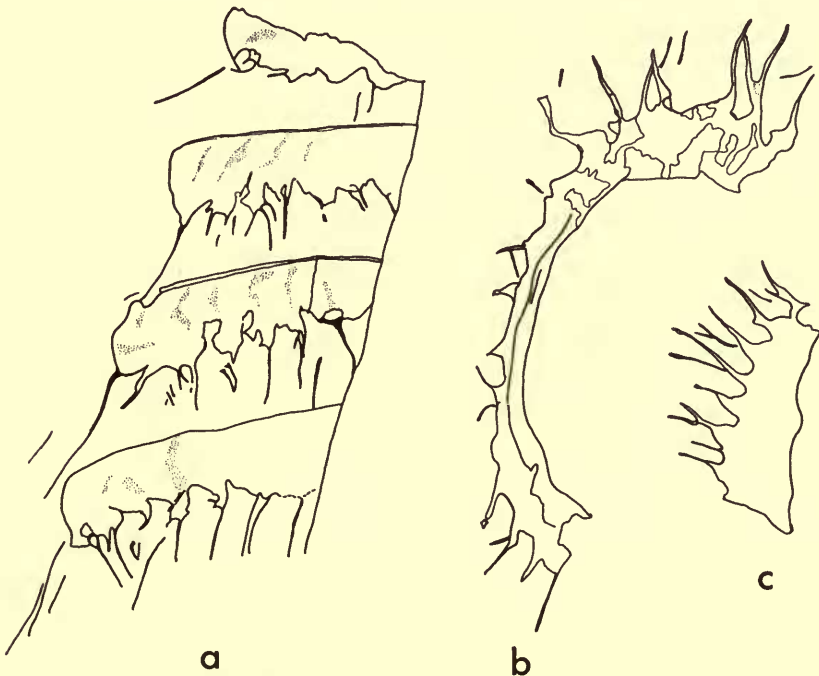


FIG. 36. a-c, *Monograptus turriculatus* (Barrande), specimens suggesting complicated spinose apertural processes; respectively GSM RS6614, LU 57699, LU 57695; *turriculatus* Zone, Cross Fell (a) and Pull Beck, Lake District; all figures  $\times 12\frac{1}{2}$ .

like shape, it is true, but there is in the Russian *turriculatus* Zone faunas a species like *M. exiguus* in rhabdosome shape but with *undulatus* thecae. Such a species would have made a perfect ancestor for *Sinodiversograptus*.

*Diversograptus* probably originates in the *magnus* to *argenteus* Zones through one of the early *Monograptus* s.s. species discussed above, p. 58. Certainly the Manck type collection has specimens ranging from about this level up to the *crenulata* Zone. Very few species are involved in the opinion of Rickards (1973) who broadly divided them into *D. capillaris* (Carruthers) below and *D. ramosus* Manck at the top of the sequence. The evolution of *Diversograptus* from *Monograptus* s.s. required a degree of gracilization as well as cladia production. The fact that thecal cladia are produced suggests that its ancestor would probably have exhibited a *lobiferus*-type hook with its ventrolaterally directed processes, and was not likely to have been *M. undulatus*, which apparently lacks such processes.

*Barrandeograptus* Bouček (1933) is included here as a Llandovery cladia-producing genus with few species. Its nature is very poorly known. If the apertures are really introverted as indicated by Bouček & Přibyl (1952) it is possible that *B. pulchellus* (Tullberg) evolved from a species of *Pribylograptus*, although there is a considerable time lag between the two genera (Fig. 1).

38. '*Spirograptus*'. None of the species normally included in *Spirograptus* (e.g. Přibyl 1945) are known in any detail. *M. turriculatus*, the type species, has a spirally coiled rhabdosome (Fig. 36) with 'hooked' thecae and thecal spines (? more than two to each theca); other species included by Přibyl only have variable coiling and 'hooked' thecae as unifying characters. As a genus it is valueless, serving only to indicate that from the *turriculatus* Zone upwards in the Llandovery a lot of monograptid (*sensu lato*) species became variously coiled. Not surprisingly the evolution of included forms is unknown and will require a great deal of work on the thecal morphology. Some 'typical' *Spirograptus* species (e.g. *S. tullbergi*)

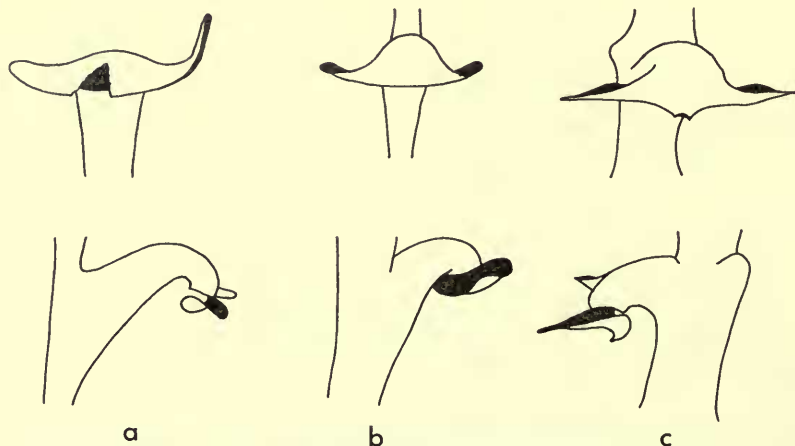


FIG. 37. Idealized sketches depicting similarity of thecal structure in *Monograptus spiralis* (a), *M. formosus* (b) and *M. exiguus* (c): these have respectively been referred to the genera *Oktavites*, *Monograptus* s.s. and *Streptograptus*. All figures  $\times 20$  approx.

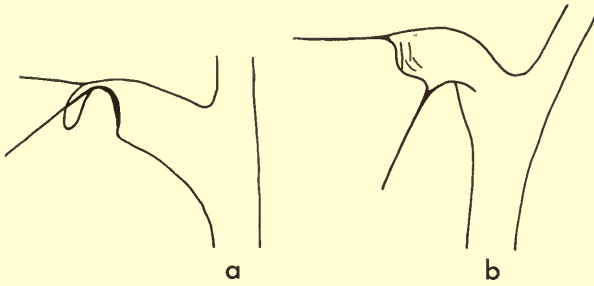


FIG. 38. Thecal structure of *M. delicatulus* Elles & Wood taken from isolated Russian specimens, courtesy of Alexandre Obut ;  $\times 25$ .

could readily be included on present evidence in *Campograptus*, *Oktavites*, *Spirograptus* or *Monograptus* s.s.

39. *Oktavites*. As far as we are concerned, Levina's (1928) genus includes only the type species *M. spiralis* and probably *M. exiguus* (Pl. 2, fig. 6), which although having a ventrally curved, fish-hook rhabdosome, has thecae very similar indeed to those of *M. spiralis* (Fig. 37). It is probable that some of the species at present placed in *Spirograptus* by some Continental workers actually belong here with *M. spiralis*. As with spirograptids the evolution is unknown at present, but Sudbury (1958) has suggested that *M. spiralis* evolved from the triangulate monograptid *M. delicatulus*. Although we agree with her this is in the right region of the plexus, isolated specimens of *delicatulus* (Fig. 38) suggest that the spines are too highly developed for it to be the actual ancestor of *M. spiralis*.

*M. exiguus* may have evolved similarly but has also been involved in the tendency, common from the *turriculatus* Zone upwards in the Llandovery, to produce a ventrally curved fish-hook rhabdosome. *M. spiralis*, and possibly other 'spirograptids', may have been ancestral to some *Cyrtograptus* species (p. 76).

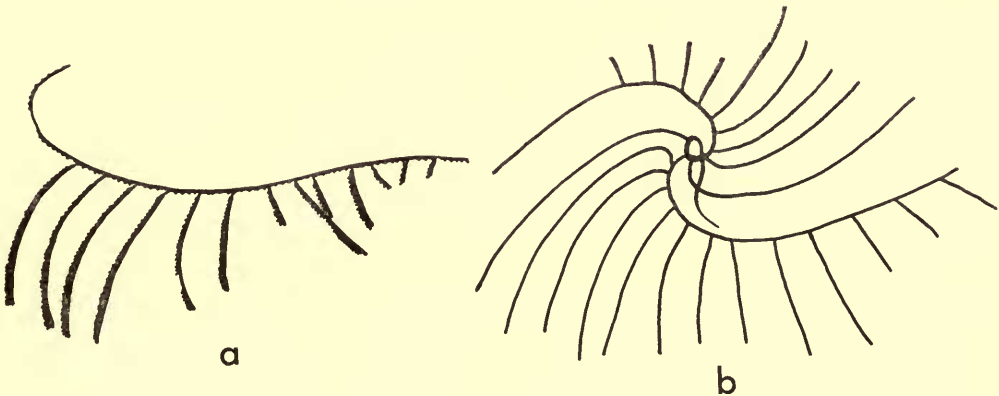


FIG. 39. a, *Uvalograptus*, after Koren' (1962). b, *Averianowograptus* diagrammatic after Obut (1949) and authors' examination of original specimens,  $\times \frac{1}{2}$ .

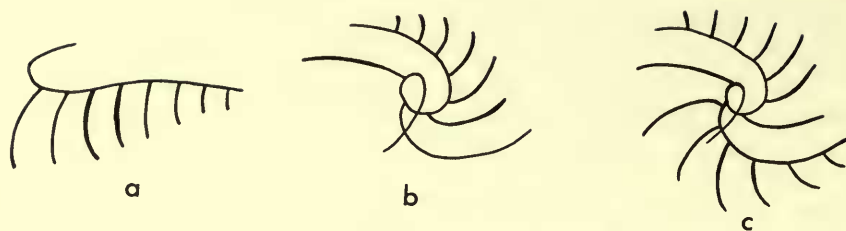


FIG. 40. Depicting manner in which *Uralograptus insuetus* (a) may have given rise to *Averianowograptus magnificus* by enrolling of the proximal end as in b, and then infilling of the gap created between the first two cladia by growth of secondary cladia on the second primary cladium (c). All figures approx.  $\times \frac{1}{4}$ .

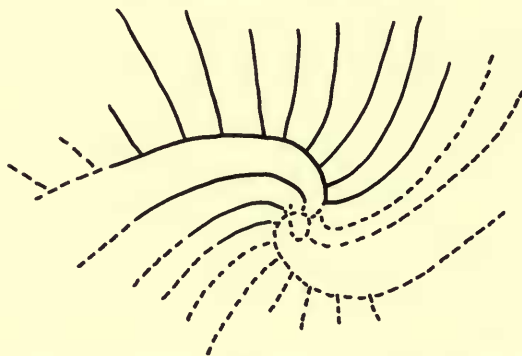


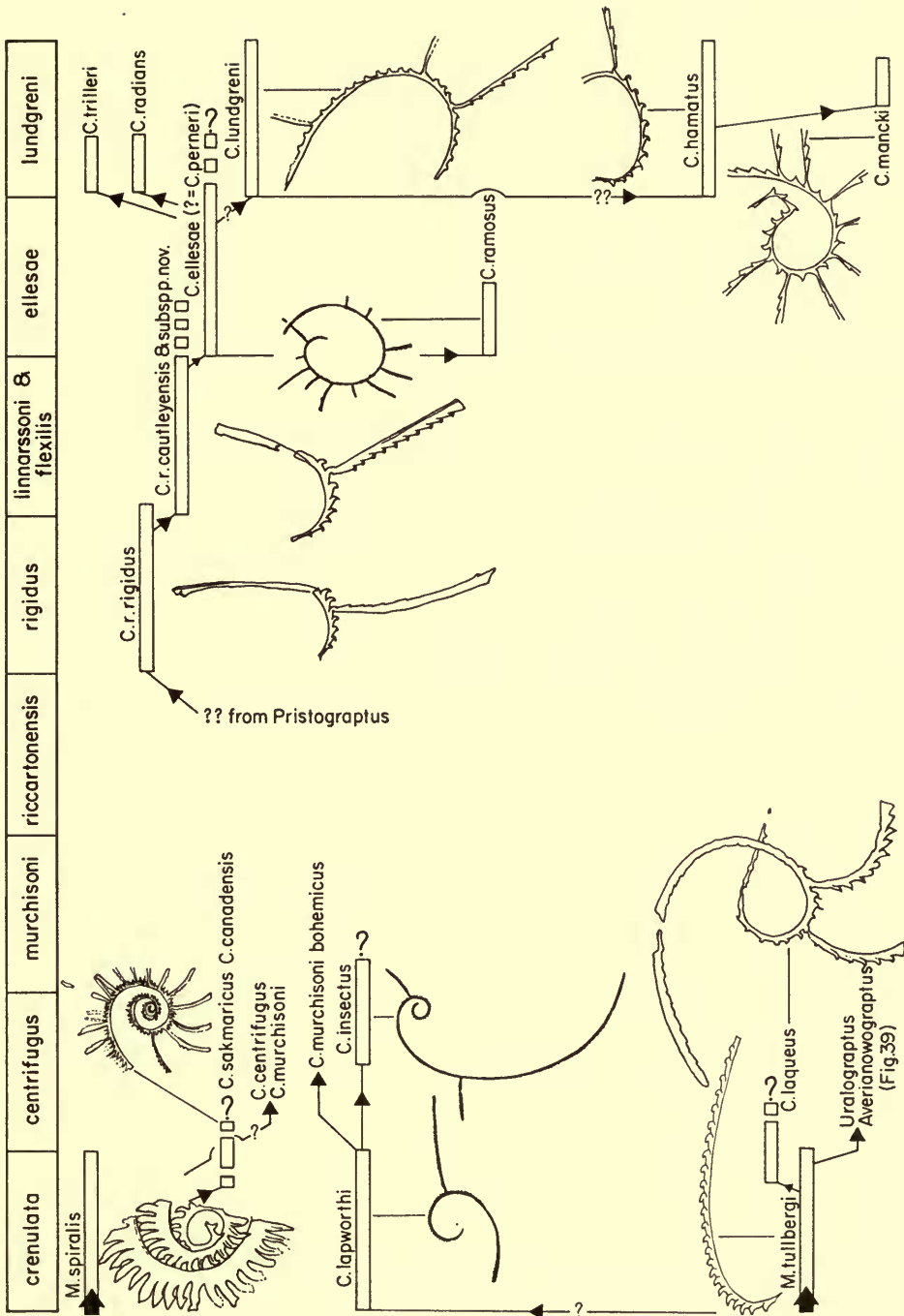
FIG. 41. Diagram depicting suggested relationship of the genus *Damosiograptus* Obut (1949), solid lines, to *Averianowograptus* Obut (1949), dotted lines plus solid lines;  $\times \frac{1}{2}$  approx.

40. *Averianowograptus* and *Uralograptus*. These two genera are typified by extremely long, slender proximal regions, hardly coiled at all, and which have axially elongate, small, slender hooked thecae. Whilst the main stipe of *U. insuetus* Koren' maintains this growth, and in the more distal regions produces numerous cladia from the hooked thecae, that in *A. magnificus* (Averianow) takes a tight coil (presumably a helical spiral) after several centimetres growth and only then produces cladia (Fig. 39). This, and the fact that in *A. magnificus* only the second cladium produced secondary cladia, is the main difference between this genus and the robust *Cyrtograptus* species such as *C. centrifugus* (p. 76).

As a purely speculative suggestion it is possible that *Averianowograptus* has evolved from *Uralograptus* by the latter developing a spiral coil between or about

FIG. 42. Evolution of *Cyrtograptus* and related genera: *M. spiralis* after Jackson & Etherington (1969),  $\times 2\frac{1}{4}$ ; *C. sakmaricus* after Koren' (1968),  $\times 0.45$ ; *C. lapworthi* and *C. insectus* after Bouček (1933),  $\times 0.45$ ; *M. tullbergi*, HUR S97.5.5/11,  $\times 1\frac{3}{4}$ ; *C. laqueus* after Jackson & Etherington (1969),  $\times 1\frac{3}{4}$ ; *C. rigidus rigidus*, SM A75341,  $\times 1\frac{3}{4}$ ; *C. rigidus caulleyensis*, SM A55217,  $\times 1\frac{3}{4}$ ; *C. ramosus* after Bouček, (1933),  $\times 0.45$ ; *C. lundgreni*, SM A75269,  $\times 1\frac{3}{4}$ ; *C. hamatus*, GSM 10719,  $\times 1\frac{3}{4}$ ; *C. mancki*, after Bouček (1933),  $\times 1\frac{3}{4}$ .





the position of its first and second cladia : such a change would open a gap between those cladia which could be filled by secondary cladia off the second primary cladium (Fig. 40). *Damosiograptus* Obut (1949), the type specimen of which has been examined by one of us (R. B. R.), is a junior synonym of *Averianowograptus* (Fig. 41). It is possible that *Averianowograptus* has been somewhat superfluously split off from *Cyrtograptus* for there are some undoubted *Cyrtograptus* species which have relatively open proximal coils (*C. insectus* Bouček, *C. lapworthi* Tullberg).

41. *Cyrtograptus*. The oldest cyrtograptids, those of the latest Llandovery and earliest Wenlock, appear to include at least three main lineages, all of which may have developed from the *spiralis* complex. *M. spiralis* itself occurs in abundance in late Llandovery age rocks in many parts of the world (see Jackson & Lenz 1962, Obut, Sobolevskaya & Bondarev 1965, Obut & Sobolevskaya 1966, Jackson & Etherington 1969, Teller 1969, Berry & Murphy 1974) and exhibits some morphological variation, from one locality to another, in tightness of coiling and at least the apparent degree to which the thecae are hooked. When flattened specimens of *spiralis* have been compared closely with the proximal parts of highly coiled late Llandovery cyrtograptids such as *C. sakmaricus* Koren' (Berry & Murphy 1974) little difference between them may be noted. Indeed, the similarities suggest that a local population of *M. spiralis* was probably ancestral to that stock of late Llandovery and early Wenlock cyrtograptids which have highly and relatively tightly coiled proximal regions (*C. sakmaricus* Koren', *C. canadensis* Jackson & Etherington, *C. coroniformis* Golikov, *C. shishkaticus* Golikov, *C. centrifugus* Bouček, and possibly *C. murchisoni* Carruthers).

A second stock of latest Llandovery-earliest Wenlock cyrtograptids is exemplified by *C. lapworthi*, which has a relatively openly coiled proximal region and a single cladium that commonly develops from a theca on the most highly curved part of the main stipe. The main stipe commonly widens relatively rapidly. Specimens of *C. lapworthi*, the oldest member of the stock, are widely found and commonly numerous. They exhibit a relatively high degree of morphologic variation in rate of widening and degree to which the thecae are hooked in the proximal part of the rhabdosome. Some specimens appear similar to *M. planus*. The *C. lapworthi* lineage may have developed from *planus* or a *planus*-like form.

The third stock that appears to be present among the latest Llandovery-earliest Wenlock cyrtograptids is exemplified by *C. laqueus* Jackson & Etherington and *C. parvulus* Golikov. These have a relatively open coil and relatively few (commonly two to five) cladia. Proximal ends are characteristic, being straight and relatively thin and widening relatively slowly. The stock could have developed from *M. tullbergi* or a similarly openly-curved 'spirograptid'.

After a modest initial burst in stocks and number of species in the latest Llandovery-earliest Wenlock interval, cyrtograptids appear to have declined remarkably. No species has been recorded from the *riccartonensis* Zone, at least in those parts of the world in which it may be recognized. Coeval strata in the Urals and western North America (Yukon, Nevada) bear somewhat different graptolite associations than in Europe (Jackson & Etherington 1969, Berry & Murphy 1974).

Strata in western North America and the Urals that *may* be coeval with the essentially European *riccartonensis* Zone do bear a few cyrtograptids, which appear to be of the *C. lapworthi* type.

The marked reduction among cyrtograptids at about the interval of the *riccartonensis* Zone of the early Wenlock is followed by appearance of the *C. rigidus* lineage the origin of which is in doubt (Fig. 42). The earliest forms in this lineage (*C. r. rigidus*) may have the cladium developed from th4. Cladial development is delayed to later thecae in stratigraphically higher members of the lineage. A possible ancestral species may have been lacking in cladia and possibly even thecal hooks. Trends in the *C. rigidus* line include both delay of the cladium and gracilization of the stipes (*C. perneri* and *C. hamatus*, for example). Species with many cladia and relatively tightly coiled rhabdosomes (*C. radians* Törnquist and *C. mancki* Bouček) may have developed from members in the *C. rigidus* lineage in the latter part of the Wenlock. Such coiled species with many cladia were short-lived.

The cyrtograptids appear to have been polyphyletic with at least four and possibly more basic stocks present within the currently recognized genus *Cyrtograptus*. Fig. 1 (p. 7), which shows the approximate number of species at each horizon, by itself suggests a polyphyletic origin for *Cyrtograptus*.

42. *Saetograptus* and *M. ludensis*. The pristiograptid stock outlined above (p. 67) probably gave rise through *M. ludensis* to *Colonograptus colonus* and *Saetograptus varians* and hence to *S. chimaera*. The detailed morphology of these forms has been described by Walker (1953), Urbanek (1958), Hutt (1969) and Holland *et al.* (1969). The beginning of the lineage involves the acquisition by

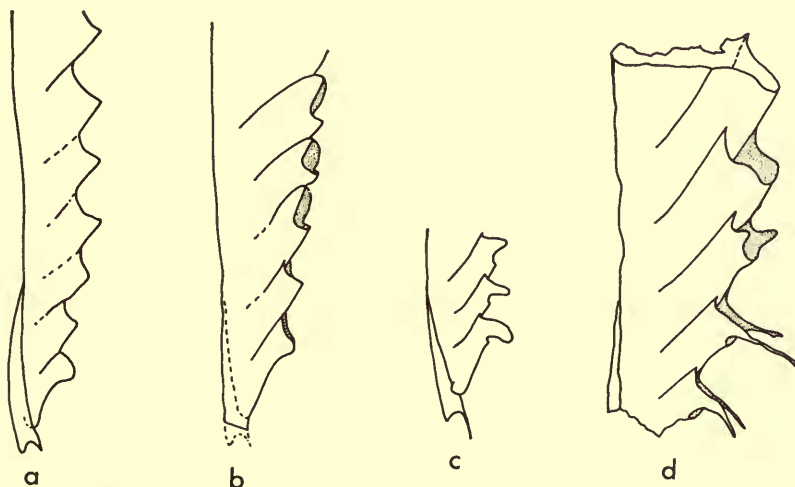


FIG. 43. a, b, '*Monograptus*' *ludensis*, respectively TCD 8658 and SM A60905; c, *Saetograptus* [*Colonograptus*] *colonus*, after Bulman (1970); d, *Saetograptus* (*Saetograptus*) *variens*, after Hutt (1969). Suggesting progressive change of paired lappets (a, b) to elongated paired lappets (c) and then to spinose, enrolled lappets (d). All figures  $\times 12\frac{1}{2}$ .

*M. ludensis* of low paired lappets on the first and occasionally the second theca. Subsequently these became elongated in *S. colonus* and enrolled in *S. varians* and *S. chimaera* (Fig. 43). The rhabdosomes otherwise remain much the same, with distal pristiograptid thecae and slow spread of the proximal thecal type along the rhabdosome. Although it is often assumed from silhouette material that such species as *M. roemeri* Barrande and *M. leintwardinensis* Lapworth are saetograptids this has not been established from transparencies, and the work of Hutt (1969) warns of the dangers in these assumptions. More recent work by Urbanek (1970) on thecal processes in *Bohemograptus* emphasizes the point, for thecal processes need not be composed of fusellar tissue as they are in some species of *Saetograptus*. The intermediate nature of *S. varians* led Bulman & Rickards (*in* Bulman 1970) and Hutt (1969) to place *Colonograptus* Přibyl as a junior synonym of *Saetograptus* Přibyl. Saetograptids probably range into the Pridoli (*S. pilosus* Jackson & Lenz 1972 and *S. willowensis* Berry & Murphy 1974) although the detailed structure of many supposed saetograptids is not known.

43. *M. bugensis* and *M. hercynicus*. From about the level of the *ultimus* Zone upwards into the Devonian there occur a number of species which again have thecal hooks. In the case of *M. formosus* the hook is almost indistinguishable from that of the upper Llandovery species *M. spiralis* (Fig. 37, p. 72) whilst the form of the rhabdosome is close to that of some 'spirograptids' as well as to the Pridoli species such as *M. perneri* and *M. bouceki*. Others have a 'hood' from a pronounced geniculum: the hood may retreat distally so that the graptolite is biform (*M. ramstalensis* Jaeger) or it may remain throughout the length of the stipe giving an at least superficial appearance of a *Monograptus* s.s. It has been established by one of us (R. B. R.) that on specimens of *M. uniformis* from the Polar Urals this hood consists of fusellar tissue and, therefore, represents excessive growth of the dorsal thecal wall relative to that of the ventral wall.

The problem of the origin of these forms has been briefly mentioned above (p. 62), and we consider that the stratigraphic record from the *nilssoni*-*scanicus* Zone upwards through the Ludlow is not complete with respect to *Monograptus* s.s.; rather the late Silurian-early Devonian forms evolved independently from a pristiograptid ancestor.

The development of *Saetograptus* from *P. ludensis* by the evolution of paired lappets (Fig. 43) has already been demonstrated, and it is of interest that pristiograptids with lateral lappet structures on at least the proximal one or two thecae are present in Ludlow (*P. roemeri* Barrande) and Pridoli forms (*P. bugensis* Teller, *P. rarus* Teller and related species in the *P. transgrediens* Perner group). Dorsal coalescence of these lappet structures is all that is needed in some instances to evolve those rhabdosomes that have both hooded and pristiograptid thecae (biform rhabdosomes) and those in which all thecae are hooded. In other such rhabdosomes, a certain increase in geniculation is required (Fig. 44).

The position of the Ludlow 'monoclimacids' *M. haupti* (Kuhne) and *M. micropoma* (*sensu* Urbanek 1958) is worthy of note in regard to possible ancestors for certain late Silurian-early Devonian rhabdosomes with hooded thecal apertures on



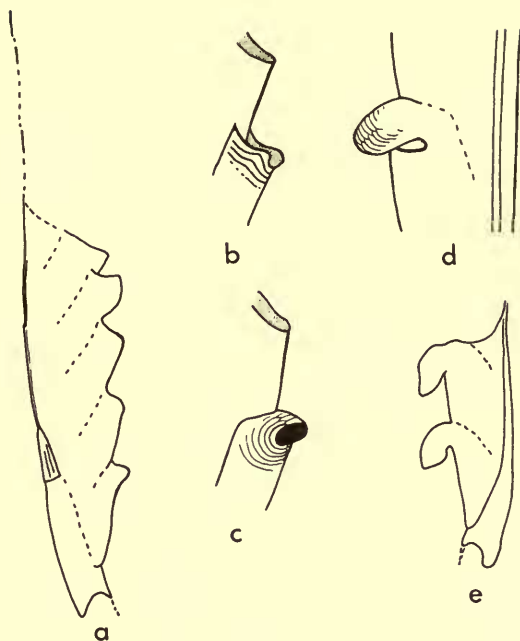


FIG. 44. Depicting the manner in which the thecal hooks or hoods of *M. uniformis* (d, e) might have developed from a paired lappet structure as exhibited by '*M.*' cf. *varus* Teller (a, b) by dorsal coalescence of the lappets (c); a, '*M.*' cf. *varus*, Romanian Geological Survey,  $\times 12\frac{1}{2}$ ; b, idealized interpretation of paired lappet structure of '*M.*' cf. *varus*; c, suggested dorsal coalescence of lappets to form a hook or hood; d, sketch of fusellar structure on thecae of *M. uniformis* made by R. B. R. in the collection of Dr Koren', Leningrad,  $\times 12\frac{1}{2}$ ; e, proximal end of *M. uniformis*, after Koren' (personal communication).

some or all thecae. *M. haupti* is known to range through most if not all of the Ludlow (Teller 1969, Urbanek 1970, Jackson & Lenz 1972). Thecae in some specimens of *M. haupti* display considerable geniculation (see Urbanek 1958) as well as curvature in the proximal part of the rhabdosome similar in degree to that among certain Pridoli and younger monograptids with thecal hoods. The thecae in early Ludlow specimens of *M. haupti* as well as the range in morphological variation in specimens from several positions in the Ludlow suggest that *M. haupti* developed from a pristiograptid, possibly during the early Ludlow. Of note in this suggestion is that no post-Wenlock 'monoclimacids' are at present known with either paired lappets or other lateral processes.

Urbanek's (1958) study of the early Ludlow 'monoclimacid' *M. micropoma* indicated that the dorsal thecal flanges or genicular projections were formed from microfusellar tissue. If this were also true for *M. haupti* and some late Silurian-early Devonian monograptids with hooded or even apparently hooked thecal apertures, then the problems involved in their ancestry would be near solution.

The earliest late Silurian-early Devonian monograptid with hooded thecal apertures is *M. balticus* Teller. It occurs in late Ludlow strata (Teller 1969,

Jackson & Lenz 1972). Specimens of the *angustidens-uniformis-hercynicus-yukonensis* plexus with thecal hoods strongly developed on the proximal thecae but, in some specimens, weakly developed on the distal ones appear stratigraphically low in Pridoli age beds (Jackson & Lenz 1969, Lenz & Jackson 1971, Jackson & Lenz 1972). A general trend among specimens of the *uniformis-hercynicus* group is for the distal thecae to be less strongly hooded than the proximal in relatively more specimens among the stratigraphically higher and thus younger members of this stock.

All thecae are apparently hooded in *M. balticus* and most are hooded in a majority of specimens of *angustidens* and *uniformis*. The early members of the *angustidens-uniformis* group may have developed from *M. balticus*. The first steps towards reduction in the amount of hood over the apertures in distal thecae were taken in some specimens in the *angustidens-uniformis* group.

The lineage *M. aequabilis-M. aequabilis notoaequabilis* Jaeger is characterized by the proximal one to three thecae having thecal hoods and those of the remainder of the rhabdosome being slightly to markedly geniculate. The hoods on the proximal thecae appear to be paired lateral lappets that have grown together. *M. aequabilis aequabilis* occurs in *M. uniformis* Zone beds (Jaeger 1959, Berry & Murphy 1974) in Europe and western North America (Berry & Murphy 1974). Its ancestry is uncertain, although it may have developed from a *P. transgrediens* group form.

*M. hemiodon* Jaeger is another early Devonian monograptid with uncertain ancestry. It has hooded proximal and strongly geniculate distal thecae. Both the *aequabilis* and *hemiodon* stocks might have developed from a *haupti*-like form in which the proximal thecae had developed paired lateral lappets that subsequently fused. No record of such a form exists, however, and the Pridoli interval separates the youngest *haupti* and the oldest specimens of the *aequabilis* and *hemiodon* stocks. Alternatively some member of the pristiograptid lineage, particularly one of the *P. transgrediens* group, or a Pridoli pristiograptid such as *P. kosoviensis* in which thecae in some specimens appear somewhat geniculate, may have been the ancestor.

*M. microdon* Richter is another latest Silurian-early Devonian form with unknown ancestry. *M. microdon* appears to have hooded thecae and a thin rhabdosome. Its thecae have hoods of approximately the same size throughout. It may have developed as an offshoot from the *angustidens-uniformis* stock early in the history of that group when thin rhabdosomes were common.

The youngest monograptids, those in the *yukonensis* group, appear to have come from the *angustidens-uniformis-hercynicus* group. A surprising degree of morphological variation has been described among members of the *yukonensis* group (Jaeger in Churkin *et al.* 1970, Jaeger *et al.* 1970, Lenz & Jackson 1971). The *yukonensis* group appears to be related to and derived from the *angustidens-uniformis-hercynicus* group through either *M. thomasi* Jaeger or *M. falcarius* Koren', or both (Koren' 1971). Stratigraphically, the former species lies above the highest *M. hercynicus* and below as well as with the lowest *M. yukonensis* (Berry & Murphy 1972). Koren' (1971) illustrated a number of rhabdosomes of *M. falcarius* that had shapes intermediate between those of the *M. hercynicus* and *M. yukonensis* group forms.

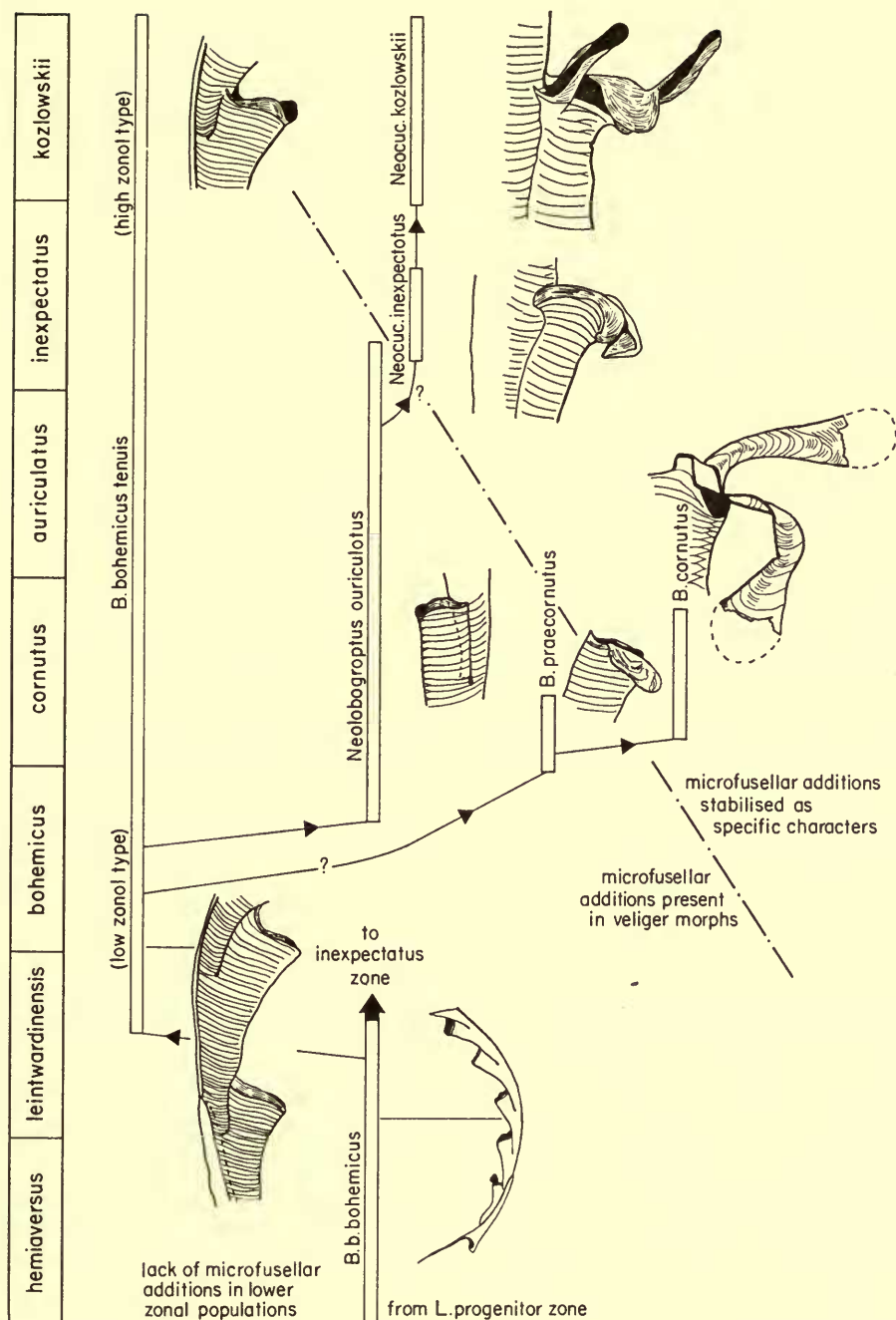


FIG. 45. Evolution of *Bohemograptus*, *Neolobograptus* and *Neocucullograptus*, simplified and redrawn after Urbanek (1970). Figures approx.  $\times 27$ .

44. *Bohemograptus*. The research of Urbanek (1970) has demonstrated that the *B. bohemicus* (Barrande) lineage extends well above the *leintwardinensis* Zone, and leads eventually (in pre-*ultimus* Zone strata) to the genus *Neolobograptus* (below) and to *Bohemograptus cornutus* Urbanek and species of *Neocucullograptus* in which the microfusellar additions become stabilized as specific characters (Fig. 45). *Bohemograptus* is characterized by ventrally curved species with modified pristiograptid thecae the apertures of which may be devoid of or provided with microfusellar additions as lobate, annular or tape-like structures. The roots of the genus probably lie among the low Ludlow pristiograptids, evolving by gracilization of a member of the main stock and the production of a ventrally curved rhabdosome. It is of interest that *B. bohemicus* appears low in the *nilssoni* Zone and yet not until post-*leintwardinensis* times does the evolutionary burst take place, thus providing a pattern parallel with monoclimacid and pristiograptid gross evolution (Fig. 1).

45. *Neocucullograptus* and *Neolobograptus*. *Neolobograptus auriculatus* Urbanek is the species of a monotypic genus providing the link between *Bohemograptus* and *Neocucullograptus*. Additions of microfusellar apertural structures had not yet become stabilized, but the genus differs from *Bohemograptus* in having strong bilateral elevations (lappets) of the thecal margin provided with dorsolateral incisions (Fig. 45).

*Neocucullograptus* evolved directly from the previous species and is characterized by advanced microfusellar apparatus (Fig. 45).

46. *Neodiversograptus* Urbanek (1963) has been discussed in great detail by that author and by Palmer (1971) and more briefly by Rickards (1973) in his re-examination of *Diversograptus* Manck. The genus evolved in the low Ludlow in much the same way as *Bohemograptus*, namely by gracilization of a member of the pristiograptid stock, but in this case producing species capable of cladia generation from the sicula (Fig. 46). These eventually gave rise to the genus *Linograptus* (below).

47. *Cucullograptus* and *Lobograptus*. The definition and evolution of these genera were described by Urbanek (1966). *Lobograptus* was essentially a simpler cucullograptid originating in the same way as *N. nilssoni* in the low Ludlow. The earliest species is *L. progenitor* giving rise to *L. simplex* and then *L. expectatus*, each with symmetrical apertural processes. Eventually lobograptids such as *L. scanicus* and *L. imitator* evolved with hypertrophy of the right apertural lobe; finally *L. cirrifer* evolved with a rostral superstructure on the apertural lobes.

Cucullograptids evolved from *L. simplex* (Fig. 47) but exhibit hypertrophy of the left lobe (e.g. *C. pazdroi*), eventually acquiring a rostral superstructure on the apertural lobes (*C. aversus rostratus*).

48. *Linograptus* and *Abeisograptus*. The Devonian genus *Abeisograptus* Hundt probably evolved from the late Silurian-early Devonian genus *Linograptus* Frech, by the development of paired thecal cladia on the procladium and central sicular



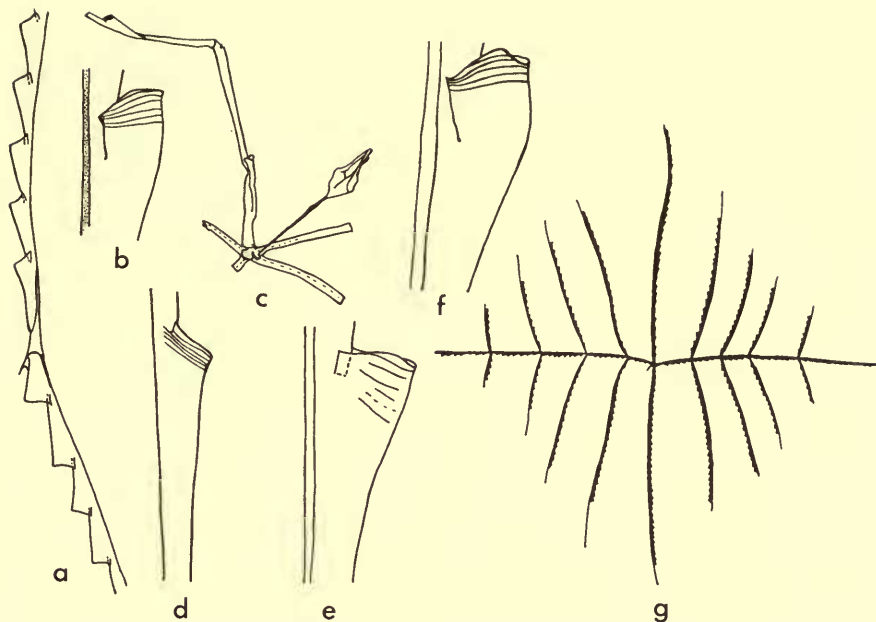


FIG. 46. Nature of thecae and cladia in *Neodiversograptus*, *Linograptus* and *Abeisgraptus*: a, *N. nilssoni*, after Palmer (1971),  $\times 6$  approx.; b, *Linograptus posthumus*, proximal theca, simplified after Urbanek (1963),  $\times 12\frac{1}{2}$ ; c, *Linograptus posthumus*, after Urbanek (1963),  $\times 7$  approx.; d, *Neodiversograptus beklemishevi*, after Urbanek (1963), proximal theca,  $\times 12\frac{1}{2}$ ; e, *N. beklemishevi*, after Urbanek (1963), distal theca,  $\times 12\frac{1}{2}$ ; f, *Linograptus posthumus*, distal thecae, after Urbanek (1963),  $\times 25$ ; g, *Abeisgraptus tenuiramossus*, after Jaeger (1959),  $\times 1$  approx.

cladium (Fig. 46). *Linograptus* has no thecal cladia, but at least one and usually several sicular cladia.

## VI. SUMMARY OF SILURIAN TRENDS

From the detailed lineages described in sections III to V above (pp. 11-83) it is possible to identify a number of 'trends', morphological changes, often affecting several distinct evolutionary lineages, biserial *and* uniserial, and quite commonly affecting them at almost the same time or for a similar span of time. The more important or conspicuous of these are summarized below. It has often been found that the *recognition* of a new morphological feature in one group has been followed rapidly by its recognition in others. A good example is that of genicular hoods of microfusellar tissue first noted in monograptids by Urbanek (1958), although known in biserials as early as 1890 (Holm), and now known in other monograptid groups in the Llandovery and Ludlow and in biserials in the Llandovery. Fig. 48 is an attempt to note the first appearance, acme and span of the main trends discussed. It is not the purpose of this paper to explain the various Silurian trends in terms of the mode of life of graptoloids, but clearly the many new features described above have some import on the question. An interpretation in terms of mode of life will be made elsewhere.

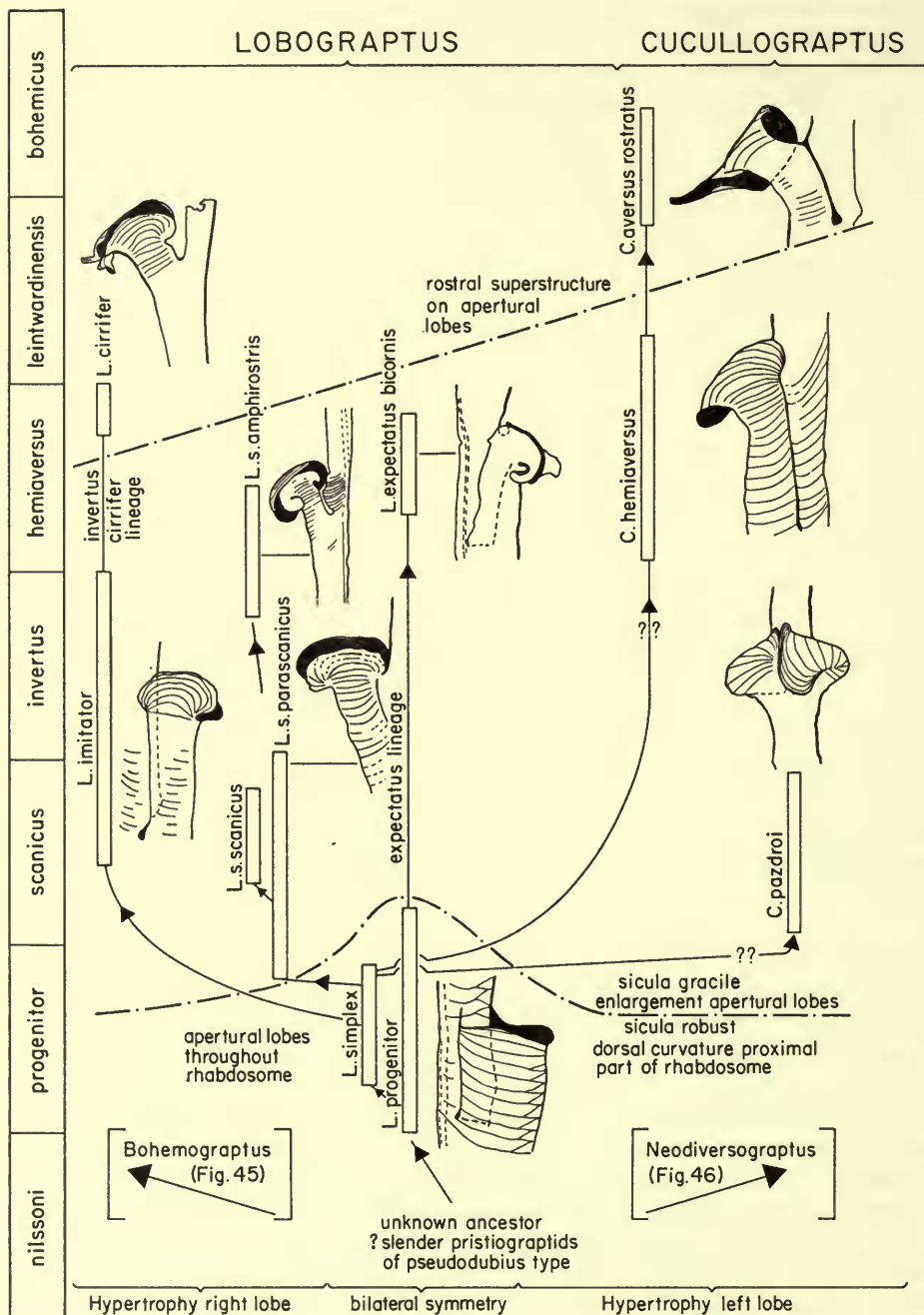


FIG. 47. Evolution of *Cucullograptus* (*Cucullograptus*) and *C.* (*Lobograptus*), simplified and redrawn after Urbanek (1966). Figures approx.  $\times 27$ .

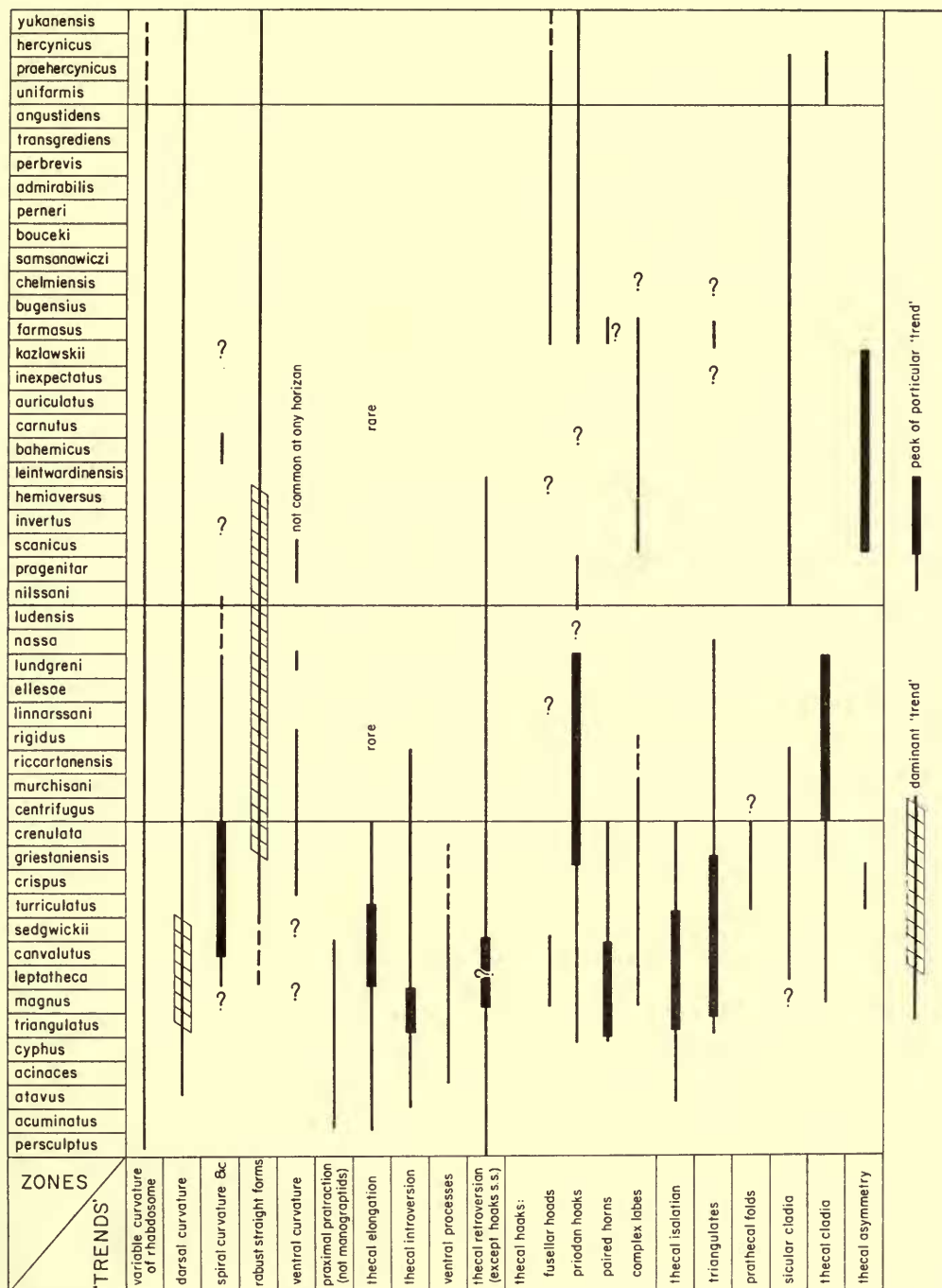


FIG. 48. Summary of the geological range, peaks and dominance of 'trends' (pp. 83-96).

## Variable Rhabdosome Curvature

Biserial scandent graptoloids such as *Glyptograptus* have stiff rhabdosomes but on achieving proximal protraction, in the form of the dimorphograptid or monograptid condition, the rhabdosome immediately becomes curved in some way. The earliest monograptids (Fig. 17, p. 37) tend to be long, slender and variously curved. Thus *Atavograptus* species and early *Pribylograptus* species such as *P. cf. incommodus*, *P. sandersoni* and *P. incommodus* have these attributes, as do the gracile members of many later (mostly robust) graptolite groups. Even a few robust species like *Pribylograptus leptotheca* are either dorsally or ventrally curved, or both, and these may be regarded as having to some extent retained the earlier state.

## Dorsally Curved and Spiral Rhabdosomes

At an early stage in monograptid evolution some rhabdosomes assumed a more or less stiff dorsal curvature (Fig. 17). The genus *Coronograptus*, which originated in the *atavus* Zone (Fig. 17), becomes either stiffly or pronouncedly dorsally curved and the rhabdosomes robust, whilst *Lagarograptus*, appearing shortly after in the *acinaces* Zone, is less robust and with a less stiff dorsal curvature. It seems to be true that the more robust graptolite species were stiffly curved, usually dorsally. Each group has one or two exceptions: *Monoclimacis continens* Törnquist and *Testograptus testis* Barrande are examples.

Pribylograptids achieved dorsal curvature with *P. argutus* in the *cyphus* Zone and dimorphograptids almost immediately (in the uniserial portion), although the earliest form, *D. elongatus*, does not always display a dorsally curved uniserial portion. In the case of dimorphograptids the presence of dorsal curvature in even quite short uniserial portions probably reflects the immediate adjustment of a vertically oriented biserial graptolite in order to maintain its vertical position in the water (Figs 49a-c). Thereafter probably most monograptid graptolites were

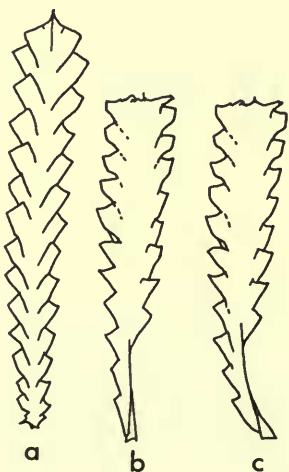


FIG. 49. Comparison of the maximum curvature seen in a fully biserial scandent species, *Orthograptus truncatus* Lapworth, (a) with that seen in the proximal end of *Dimorphograptus* (c): the situation in *D. erectus* (b), that is with a relatively straight uniserial portion, is quite unusual, and even in these cases some overall curvature is imparted by the position of the sicula. It is suggested that the curvature of the uniserial portion is an attempt to hold the centre of gravity so that the rhabdosome remains oriented vertically in the water.  $\times 5$ .



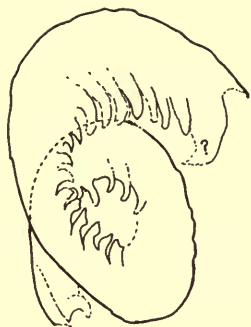


FIG. 50. *Monograptus discus* Törnquist, HUR S231,2/62, after Rickards (1970), showing a common form of preservation of the species indicating that even in short rhabdosomes curvature may have been helical rather than plane spiral.  $\times 10$ .

dorsally curved (e.g. *Rastrites*, '*Demirastrites*', '*Campograptus*' etc.) until about the *sedgwickii* or *convolutus* Zone when the proportions of other curvatures increased, including spiral rhabdosomes.

Very little research has been done on spiral rhabdosomes like those of *M. turriculatus* and *Cyrtograptus murchisoni*, but in all probability a good number of dorsally (and ventrally) curved rhabdosomes were actually conical spirals in life. *M. discus* (Fig. 50; Pl. 3, fig. 3) is one of the shortest, robust, ventrally curved species known yet the frequency with which the proximal end is found covering over the mesial portion strongly suggests a spiral rhabdosome arrangement, as do the preservational attitudes of many rastritids and demirastritids. We know of no cases where a plane spiral rhabdosome has been established, except possibly *M. convolutus* Hisinger or *T. testis* (Barrande).

It has been pointed out above (p. 73) that rhabdosomal curvature is of little guide to specific affinities, and it can be stated that most groups or genera (established on detailed *thecal* structure) usually have members which are dorsally curved and a few which are ventrally curved, or yet others which are more or less straight. However, in terms of broad evolution, the following stages were reached in the following order.

- 1, variously curved, slim rhabdosomes (often seen again in the gracile members of most groups).
- 2, dorsal curvature achieved in the *atavus* Zone and whilst maintained into the Devonian, dominant in the *triangulatus* to *sedgwickii* Zones.
- 3, from the *convolutus* or *sedgwickii* Zones upwards to the low Wenlock many spiral and many straight rhabdosomes occur (*Monograptus* s.s. and *Monoclimacis*).
- 4, from low Wenlock upwards straight monograptids, often with *slight* curvature, dominated.
- 5, in the Ludlow and above there are again slender and variously curved types (e.g. *M. microdon*), but also many stiff and more or less straight forms.

## Ventrally Curved Rhabdosomes

These are in a minority in most groups and do not appear with certainty until post-*sedgwickii* strata (e.g. '*Streptograptus*'), although some earlier spiral rhabdosomes may have essentially ventral curvature (i.e. with the thecae facing inwards within the cone as in conical dendroids): *M. involutus* is a possible early example (*magnus-sedgwickii* Zones) and *M. turriculatus* and *M. discus* are certainly later ones. After the upper Llandovery they are uncommon. Slight proximal region ventral curvature is characteristic of many pristiograptids in the Ludlow and Pridoli, as well as in some other groups. The Pridoli species *M. helicoideus* is markedly coiled.

## Proximal Protraction

Many Llandovery biserial graptolites, except retiolitids, had a tendency to produce protracted proximal ends either by achieving the dimorphograptid condition, or by lengthening the early thecae and sicula and drawing out the proximal end into a thorn-like point. The first occurrence is in the *acuminatus* Zone with *Akidograptus ascensus* and *Orthograptus? acuminatus* which achieve the result by the second method (Fig. 7, p. 19). Strictly speaking the monograptid condition itself is an example of extreme protraction, and this first occurred in the *persculptus* Zone with *Atavograptus ceryx*, a possible member of dithyrial populations.

The dimorphograptids and many monograptids appear in the *atavus* Zone, and *Rhaphidograptus toernquisti* (Fig. 8h, p. 22) may be considered a dimorphograptid with a uniserial portion of one theca only. Subsequently the tendency declines and is last seen in the lineage *Petalograptus folium* to *Cephalograptus cometa* in the *convolutus* Zone. The tendency for many biserial groups to have tiny end members (*Pseudoclimacograptus*, *Climacograptus*) is probably a process quite unrelated to proximal protraction: in the former process the whole rhabdosome becomes minute and proximal protraction only takes place secondarily and in terms of absolute measurement, *not* in relation to the rest of the rhabdosome.

## Thecal Elongation

The most extreme case known is that of *Cephalograptus cometa* where the thecae reach a length of 30 mm in some specimens. These are the longest graptoloid thecae on record and must exceed the length of many dendroid thecae, including those of *Coremagraptus*. Thecal elongation is, naturally, associated with the proximal end protraction discussed in the last section but also occurs in groups lacking this: *Pribylograptus leptotheca*, *Rastrites maximus*, *Lagarograptus acinaces* and *Monograptus singularis*. Mostly it is a Llandovery feature, with its acme in the middle of the Llandovery (*leptotheca* to *maximus* Zones), but is also known in Ludlow pristiograptids (*M. butovicensis* Bouček and *M. egregius* Urbanek), whilst lobograptids have elongate necks prior to the apertural apparatus.

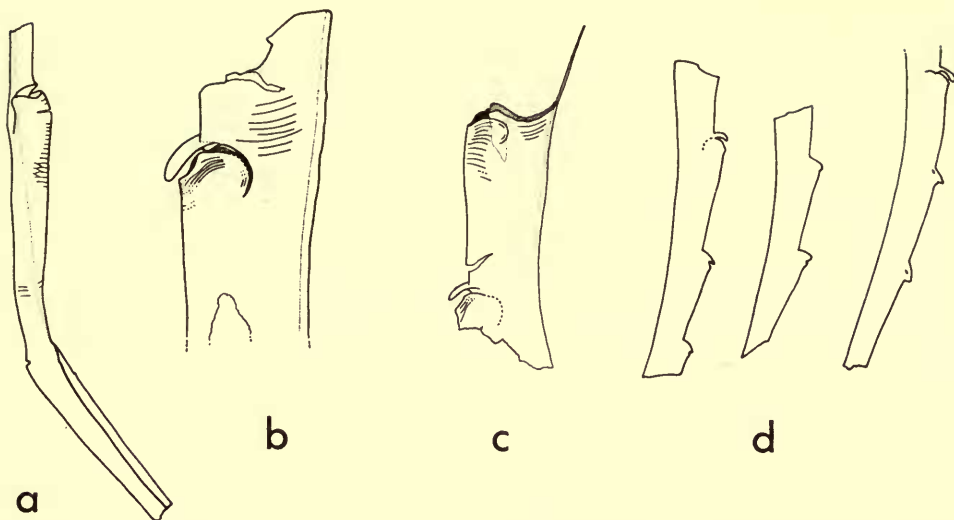


FIG. 51. a-d, *Monograptus* sp., after Hutt *et al.* (1970), showing combination of paired, lateral thecal lappets and genicular hood, the possible basic requirements for derivation of some *Monograptus* s.s. from *Monoclimacis*; Riksmuseum Cn 54882-8; a-c,  $\times 45$  approx., d,  $\times 15$ .

### Thecal Introversion

Thecal introversion has been regarded previously as a typically Ordovician feature, but it appears in the Silurian with *Pribylograptus* cf. *incommodus* (Fig. 17, p. 37) in the *atavus* Zone. Introversion in the form of paired horns and genicular hoods is confined to the genus *Pribylograptus* ranging from the *atavus* to the *sedgwickii* Zones, and to the biform *M. sudburiae* group (p. 45) from the *cyphus* and *triangulatus* Zones. *Barrandeograptus pulchellus* (Bouček & Přibyl 1954) from the *crenulata* to *riccartonensis* Zones almost certainly has introverted thecae but the structure has not been fully ascertained. Otherwise thecal introversion is seen in *Monograptus* sp. 2 (Hutt *et al.* 1970) and in *Glyptograptus* (*Pseudoglyptograptus*) spp. 1 & 2 (Rickards 1972). The former, from the *gregarius* Zone, may be related to *Pribylograptus* in that the introversion takes the form of paired lateral lappets (which may be flattened, open tubes) and a median, ventral, apertural saddle beneath a genicular hood. *G. (Pseudoglyptograptus)* has essentially everted thecae (p. 22) but the apertural margins in some (Fig. 8f) have a pronounced median process and paired lateral incisions: the ventral process itself has a slight saddle not unlike that in *Monograptus* sp. 2 (Fig. 51). The effect of this structure is to impose an effectively introverted aspect on the apertural regions only of a thecal tube which as a whole is sinuous and everted. This occurs in *G. (Pseudoglyptograptus)* in the *triangulatus* and *magnus* Zones, that is at about the acme of thecal introversion in *Pribylograptus*. The only later pseudoglyptograptid of which we are aware, *G. (P.) tabukensis* Rickards & Koren' from the *convolutus* Zone, does not display apertural introversion.

### Ventral Thecal Processes

Unless one includes the ventral apertural processes of *G. (Pseudoglyptograptus)* these structures are at present known only in *Lagarograptus*, first appear with *L. acinaces* in the *acinaces* Zone and range up to the *sedgwickii* Zone with *L. tenuis* (Fig. 17, p. 37). They are perhaps best considered as attempts to simulate thecal 'hooks' which, at these horizons, are found in a wide variety of graptoloid groups. Hence the genicular hood can be explained as a protective device over the essentially everted thecal zooid (Fig. 17). The nearest approach in other groups to the elongate ventral apertural processes of *Lagarograptus* is a slight outrolling of the ventral thecal lip, a feature clearly evolved to facilitate movement of the zooid itself into an extrovert position and similarly for it to retract with smoothness and speed.

### Retroversion

Retroversion is here considered separately from thecal hooks (below) because various structures essentially simulative of them occur in groups without true thecal hooks. The sigmoidal curvature of the thecal tube in *Cystograptus*, *G. (Pseudoglyptograptus)* and *P. (Clinoclimacograptus)*, coupled with eversion of the apertural margin, gives an overall eversion to the thecae. The zooid presumably faced outwards or ventrally during extroversion, in contrast to the ancestors of these groups where the zooid probably faced distally. Eversion to this degree (Fig. 3c, p. 14) compares with the similar eversion in *Monoclimacis* (Fig. 24, p. 55) which may be regarded morphologically and evolutionally as an early version of a thecal hook. The tendency therefore is towards eversion leading to retroversion in several groups other than monograptids. The presence of genicular hoods in other genera may be interpreted similarly: the result for the extroverted zooid would be to face ventrally or proximally as in, for example, *Climacograptus innotatus*. In others, such as *P. (Metaclimacograptus) undulatus* (Figs 3e, 4a, pp. 14-15) the situation would appear to be more flexible since the mesial part of the genicular hood is less developed and the zooid could therefore face either ventrodistally or ventroproximally. Thus the result of all these modifications can be interpreted as a *tendency towards*, if not actually achieving, the hooked condition typical of many monograptids which became, of course, the more successful group.

Thecal retroversion as interpreted above first appears with *C. innotatus* and *R. toernquisti* in the *acuminatus* Zone, and ends (monograptids excluded) with *Holoretiolites* in the Ludlow (Fig. 16, p. 35).

### Thecal Hooks

It has been pointed out by Hutt *et al.* (1972) that thecal hooks can be considered in eight different forms. Three of these have been considered above (in the sections on ventral apertural processes and retroversion, above) and the remainder are enumerated as follows.

- 1, genicular hoods of fusellar tissue, that is growth of the dorsal thecal wall but not of the lateral or ventral walls.



- 2, the *priodon* type hook.
- 3, paired horns by development of the dorsal thecal margin.
- 4, more complex hooks and lobes of fusellar tissue.
- 5, each of the foregoing could be theoretically developed as microfusellar tissue or alternations of both fusellar and microfusellar tissue.

The appearance of these hooks is included in Fig. 48, p. 85. *Priodon* style hooks may slightly precede, in the form of *M. austerus austerus* (Fig. 19, p. 43), the incoming of paired, retroverted horns exemplified by *M. austerus bicornis* in the top of the *cyphus* Zone. Genicular hoods of fusellar tissue also appear quite low in the Llandovery (e.g. *M.* sp. 1 of Hutt *et al.* 1970, *gregarius* Zone) and are still present in Devonian monograptids, although of an independent origin (p. 79). More complex lobes and hooks appear with *Monograptus* sp. B (Fig. 26) in the *magnus* Zone of the Lake District and, again, are found in the Ludlow derived from quite different ancestors. The fifth, theoretical, possibility has to be considered in view of Urbanek's (1970) work, but at present such structures are only known in Ludlow graptolites. With the exception of the fifth category, therefore, all hooks appear low in the Llandovery, and because of this, and their widespread occurrence in different groups, they may be regarded as one of the most typical of all Silurian features.

### Thecal Isolation

The earliest instance of metathecal isolation, again a typically Silurian feature, is *Dimorphograptus decussatus* from the *acinaces* Zone. In this species as in other dimorphograptids the actual nature of the aperture has not been elucidated but in profile at least the thecae of the uniserial part and the proximal thecae of the biserial part appear to have isolated apertures: more distally the thecae have the normal biserial arrangement. As far as we know, the isolation achieved by the proximal thecae of the biserial portion in *D. decussatus* is the only instance of biserial thecal isolation.

The most well-known instances of metathecal isolation are to be found in the 'demirastritids' and *Rastrites* species where the metathecal tubes of the thecae grow at right angles to the main growth direction of the rhabdosome and develop from extremely slender prothecal tubes (which Schauer (1967) incorrectly terms the *virgula*). Isolation of this kind is seen as high as the *griestoniensis* and *crenulata* Zones where the 'demirastritids' die out. The last known *Rastrites* species are in the *turriculatus* Zone.

However, metathecal isolation is also seen (Fig. 26) in non-rastritiform monograptids such as the long-ranging *M.* sp. of Hutt (p. 58). In this species the prothecal tube is just as slender as in *Rastrites* but the metathecal portion, instead of standing at a high angle to the rhabdosome, actually forms a fairly normal *priodon*-like hook on a much expanded late prothecal tube.

In a sense metathecal isolation is also achieved by the *M. knockensis*-*M. singularis* line even though the late metathecal part, and thus the aperture itself, doubles back and faces the prothecal tube (Fig. 27, p. 59). *Coronograptus*

*gregarius* occasionally exhibits late metathecal isolation, but it is not normally a feature displayed by graptolites with simple thecal tubes: all the above forms except *C. gregarius* and *D. decussatus* have 'hooked' thecae of some kind. The acme, judging on number of species, is about the *triangulatus* to *sedgwickii* Zones, perhaps slightly towards the bottom end of this range.

### Thecal Triangulation

The importance of triangulate monograptids in the evolution of Llandovery graptolites was admirably demonstrated by Sudbury (1958). Her suggested lineages and others are described above on pages 42, 44, and 45-47: although typical of several groups, on present knowledge thecal triangulation is restricted to the monograptids and like true thecal hooks is one of the few trends so restricted. Moreover the groups affected may well be quite closely related genetically and have their origins in the *M. austerus* group. The earliest species showing any kind of thecal triangulation is *M. difformis* which Hutt (1974) has established as being a top *cyphus* Zone species probably possessing simple thecal hooks. The mesial thecae of *M. difformis* are distinctly triangular (Fig. 19, p. 43). This is of considerable interest in that we normally think of new characters being introduced either proximally or distally: in the case of the triangulate monograptids it is said that the proximal introduction and spread of isolated thecae results eventually in *Rastrites* (p. 47). But triangulate monograptids such as *M. triangulatus* and *M. fimbriatus* invariably have at least one axially elongate non-triangular theca at the proximal end. Thus thecal triangulation is almost certainly directly related to the acquiring of a strong dorsal curvature by the rhabdosome, the triangular thecae first appearing at the point of maximum curvature and spreading *proximally and distally* as the curvature increases. Such arguments cannot be applied to thecal isolation which occurs in more or less straight species such as *M. capulus* and *R. equidistans spengillensis*.

The range in time of triangular thecae is from the top of the *cyphus* Zone to the *crenulata* Zone, but continues in modified form in species of *Cyrtograptus* throughout the Wenlock. Subsequently triangular thecae reappear as *M. formosus* (Fig. 37, p. 72) in the *ultimus* Zone of the Pridoli and although the origin may be quite different (p. 78) the reason may be the same, namely the acquisition of a strong dorsal curvature by the rhabdosome, particularly in its mesial regions. It is difficult to define an acme for the triangulate monograptids since, unlike those species exhibiting thecal isolation, they span a longer period, but undoubtedly triangulation is more widespread in the Llandovery than later.

### Gracile and robust rhabdosomes

A common tendency amongst monograptid groups in particular is to produce both very slender and very robust rhabdosomes, the former commonly just after the inception of the group and the latter more commonly at a later date. In other words groups or genera often have more relatively slender species at the beginning of a lineage, the later representatives being generally more robust. The *lobiferus*

lineage forms a good example originating through *M. undulatus* and *M. sp. A* (Fig. 26, p. 57) from the slender *Atavograptus*, but eventually leading to *M. lobiferus*, *M. knockensis* etc. Similarly the *priodon* lineage is represented in the Wenlock by several broad species including a form of *M. flemingii* with a dorso-ventral width of well over 4 mm (Bulman 1965). Early forms of *M. priodon* are commonly quite slender (*M. parapriodon*) and the origins of the genus probably lie in slender forms of *Monoclimacis*, a genus also producing more robust species in the Wenlock than in the Llandovery. However, the *priodon* lineage does produce at an early stage (*turriculatus* to *griestoniensis* Zones) extremely robust graptolites such as *M. sp. A* of Bassett & Rickards (1971) which might easily be confused, in a monotypic collection, for the Wenlock species *M. flemingii*. By way of contrast the *lobiferus* lineage evolved *M. sp. B*, a most slender and well-advanced form (Fig. 26, p. 57) at the very beginning of the line (*magnus* Zone). *M. gracilis* is an early offshoot of the *Atavograptus* lineage (Fig. 17, p. 000) whilst *M. angustus* and *M. fragilis* are probably similarly referable to the genera *Pribylograptus* and *Atavograptus* (or *Pristiograptus*) respectively.

However, the above 'rules' are not absolute and there is also an undoubted tendency, well displayed by the *Pristiograptus dubius* line, to evolve short-lived slender and broad species at fairly regular intervals throughout the long range of the species from the *riccartonensis* Zone into the Ludlow. Even *Pristiograptus*, however, originates through slender species and tends to produce its most robust species in the Wenlock and Ludlow: it is of interest that the few Ludlow slender 'pristiograptids' should have been capable of such spectacular evolution (Figs 45-47 and pp. 82-83). *Monograptus* and *Monoclimacis* both originate from relatively slender species, secondarily produce slender species high in the Llandovery ('*Mediograptus*' and *M. griestoniensis*) and reach a peak of robustness in the Wenlock. The triangulate monograptid plexus may display similar tendencies to those described above.

Another example of the general pattern of early species in a lineage to be somewhat more slender than the later is seen in the *angustidens-uniformis* and *hercynicus* group lineages. The early members of the *angustidens-uniformis* group (*M. balticus* Teller, *M. angustidens* Přibyl and forms closely similar to it) are more slender than *M. uniformis*. Similarly, the early members of the *M. hercynicus* group (*M. birchensis* Berry & Murphy and *M. praehercynicus* Jaeger) are more slender than *M. hercynicus hercynicus* Perner and *M. hercynicus nevadensis* Berry. Berry & Murphy (1974) have documented the stratigraphic ranges of the slender and more robust members of the *hercynicus* group in Nevada, and Jackson & Lenz (1972) have indicated the stratigraphic ranges of the gracile and robust members of the *angustidens-uniformis* group in the Yukon, Canada. In addition, the oldest representatives of the *P. transgrediens* group (*P. bugensis* Teller and *P. chelmiensis* Teller) are more slender than the later members of that group (*P. transgrediens transgrediens* Perner). The generalized trend towards robust forms from gracile members early in the history of a lineage continues among Pridoli and early Devonian stocks, although there are exceptions to the general trend (such as *M. telleri* Lenz & Jackson among *hercynicus* group members).



### Prothecal Folds

Prothecal folds are a typical Ordovician structure occurring, for example, in a number of didymograptid (*sensu lato*) types and in some *Dicellograptus* species, but homologous structures have recently been discovered in Silurian monograptids (Hutt *et al.* 1970). In uniserial scandent species the dorsal wall of the rhabdosome is marked by the nema: this is not involved in the prothecal fold but the prothecal tube forms paired bulges to each side of the nema (Fig. 37, p. 72) as well as betraying a distinct kink or bulge in the ventral wall. At present prothecal folds are known in such species as *M. exiguus* which, based on the nature of the apertural hook, has similarities to *M. spiralis*, and in *M. nodifer* and possibly other 'streptograptids' and 'mediograptids'. Thus the feature may occur in different groups at about the same time, namely *turriculatus* Zone to basal Wenlock, but as yet no evolutionary significance has been detected. The Silurian prothecal folds must, however, have originated independently in the Silurian and cannot have been derived from Ordovician dicellograptids possessing analogous structures. Undoubtedly more species will be found to exhibit prothecal folds when satisfactorily preserved material is to hand: at the moment the known species are slender, with 'hooked' thecae, and have either strong ventral or strong dorsal curvature.

### Thecal and Sicular Spinosity

The relatively late members of many Silurian lineages display thecal spines. For example, it has been suggested above (p. 49) that *M. sedgwickii* evolved from a triangulate monograptid ancestor by straightening of the rhabdosome and development of thecal spines: *M. halli* the suggested successor to *M. sedgwickii* displays a degeneration of the same basic structure. Similarly *M. pseudoplanus* displays paired horns or tubes which in the suggested descendant (Sudbury 1958) have degenerated to very short spines. Other late triangulates also develop long spines (*M. delicatulus*, Fig. 38, p. 73) as do some of their derivatives towards the end of their lineages (*M. turriculatus*, *M. spiralis*, *R. phleoides*). Indeed in those species belonging essentially to the triangulate monograptid plexus long spines are usually achieved in the *convolutus* and *sedgwickii* Zones and thereafter degenerate: the exception, *M. spiralis*, may well have evolved further into *Cyrtograptus* species in which the long spines became the pseudovirgulae of the cladia.

The *Monograptus* s.s. group most certainly developed spines in its later species such as *M. flemingii*, and these developed from the dorsolateral apertural processes of earlier species such as *M. marri* and *M. priodon*. However, the *priodon* line not only developed extremely robust rhabdosomes (*M. sp. A* of Bassett & Rickards 1971) at a quite early stage but these also exhibited considerable thecal spinosity and as far as is known at present had no successors with degenerative spines.

The genera *Orthograptus* and *Glyptograptus* also evolved thecal spines, again essentially in the later species, although in the case of *Glyptograptus serratus barbatus* and '*Comograptus comatus*' they are restricted to the proximal thecae and are strongly pendant and perhaps not all apertural in origin. In *G. serratus barbatus*



there are undoubtedly sicular (apertural) spines also, as in some species of *G. (Pseudoglyptograptus)* (Rickards & Koren' 1974). The spinosity of these genera is achieved in the *magnus* to *convolutus* Zones, that is rather earlier than in the triangulate monograptids, which in turn is earlier than in the *Monograptus* s.s. species.

A majority of Silurian graptoloid groups did not produce spinose species, and the spinose 'thecae' of some retiolitids are too little known to be commented upon further at present.

### Sicular Cladia

Sicular cladia first appear quite low in the Llandovery (possibly *magnus* Zone) in *Diversograptus* species (Rickards 1973) and occur in the upper Llandovery in *Diversograptus*, *Sinodiversograptus* and probably *Barrandeograptus*, the last ranging up into the Wenlock (p. 72). Although in regenerated, bipolar rhabdosomes the nema is also regenerated to grow along the dorsal wall of the new stipe, in the above genera the dorsal wall presumably lacks a nema since the virgella is enclosed in the *ventral* wall of the first theca of the new stipe, and there is no evidence at present of a dorsal sicular spine having been produced. The latter is, however, a possibility.

No other groups with sicular cladia have been detected in the Wenlock, *Barrandeograptus pulchellus* being essentially a survival from the Llandovery, and sicular cladia are not seen again until the genera *Neodiversograptus*, *Linograptus* and *Abeisograptus* which span the low Ludlow to low Devonian. These three genera are closely related (Urbanek 1963) but are quite removed genetically from the high Llandovery genera just discussed. In the late Silurian forms a dorsal sicular spine or spines forms the dorsal edge of the new stipe or stipes whilst the sicular aperture usually remains open. The late Silurian and Devonian genera form an undoubted lineage, but the status of the Llandovery genera *Diversograptus* and *Sinodiversograptus* has recently been called into question by Rickards (1973) who found sicular cladia in a number of quite different Llandovery groups and concluded that the feature was a late stage of astogeny potentially achievable by many groups.

### Thecal Cladia

The presence of thecal cladia in the genera *Diversograptus*, *Sinodiversograptus* and *Barrandeograptus* confers upon them a value not given by the mere presence of sicular cladia, but the possibility does remain that these also are potential late astogenetic growth stages of several groups. The genus *Cyrtograptus*, however, originating in the highest Llandovery strata (Bouček 1933; Jackson & Etherington 1969), forms a sizeable evolutionary plexus in the Wenlock with several (poorly studied) main lineages (p. 76): there are no accompanying, similar graptolites *without* cladia as commonly the case in the upper Llandovery with *Diversograptus* etc. The same arguments that are applied to *Cyrtograptus* may also be applied to the early Devonian *Abeisograptus* which is the next genus to exhibit thecal cladia. Thus all three groups originated quite independently, at different times, and each

probably has a quite different evolutionary status and value. There are few *Abeisgraptus* species, and many *Cyrtograptus* species.

### Thecal Asymmetry

Despite the common assertions of Elles & Wood (1901-18) of thecal asymmetry in Silurian monograptids the only records of which we are aware are *M. proteus* Barrande in the Llandovery (Hutt *et al.* 1970) and the Ludlow species of *Cucullograptus* (1966) and *Bohemograptus* (1970) described by Urbanek. The latter genera have asymmetrical development of processes or of the lateral apertural thecal lappets, whilst *M. proteus* displays a pronounced torsion of the thecal axis (Fig. 52). Thus only the asymmetry described by Urbanek falls into a clear evolutionary setting, and we suggest that on present evidence *M. proteus* represents a single, unusual side line of the triangulate monograptid lineage from *M. pseudoplanus* (Sudbury 1958) to *M. planus*.

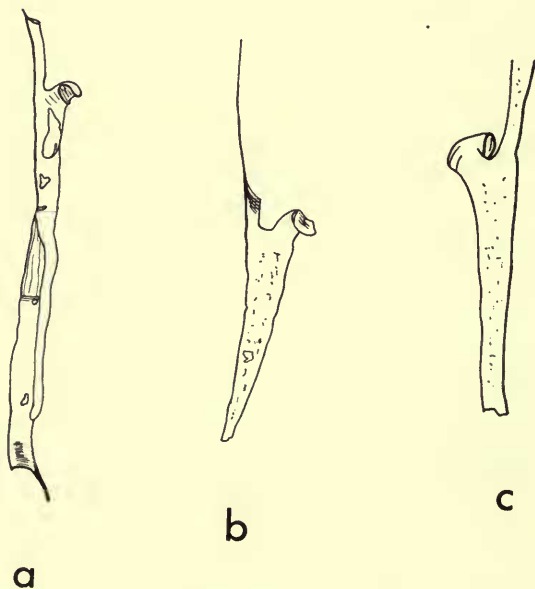


FIG. 52. a-c, *Monograptus proteus* (Barrande), Riksmuseum Cn 54934-6,  $\times 40$ , after Hutt *et al.* (1970), showing the only known case of pre-Ludlow thecal asymmetry, and the only case involving torsion of the thecal axis.

### VII. SYSTEMATIC SECTION

The classification of graptoloids has been extensively discussed in recent years and authoritative papers published by Bulman (1955, 1963, 1970) and Jaanusson (1960) in particular. There has been a large measure of agreement concerning the classification of Silurian graptoloids, with perhaps the greatest discrepancy of views on the subject of the classification of *Monograptus*. Recent approaches to this

particular problem have been described by Urbanek (1958) and by Bulman & Rickards (*in* Bulman 1970), whilst Rickards (*in press*) redefines several Llandovery graptoloid genera. In this work we have found it easy to follow the broad features of the classification of Bulman (1970), but the evolutionary studies themselves necessarily suggest some changes in detail; at the same time we have baulked at the prospect of defining several new genera for the reasons expressed above, namely that there are considerable areas, in the upper Llandovery in particular, needing a great deal of further study. We give below, in the form of systematic notes, comments upon various genera and species where we have something new to add relevant to the evolutionary story of sections III to VI. No new morphological terms are introduced; thecal spacing measurements are taken in the manner recommended by Packham (1962) in which a small number of thecae are measured and this figure translated to a 'thecae per cm' value. Location of illustrated specimens is given on the captions to the figures, both in the main text and on the plates.

Order GRAPTOLIDEA Lapworth 1875

Genus *CLIMACOGRAPTUS* Hall 1865

*Climacograptus innotatus pacificus* Ruedemann 1947

(Fig. 2, p. 12)

The subspecies is clearly close to the typical subspecies in general dimensions, being rather broader (1.5 mm exclusive of spines) and having a higher thecal spacing (20 in 10 mm as compared with 15–16 in 10 mm). However, the genicular process certainly consists of a pair of spines rather than a genicular hood, and it may eventually be necessary to raise *pacificus* to specific status. The subspecies occurs in the *complanatus* Zone in N. America, probably towards the top of that zone, and it is in keeping with the ideas expressed above that a more robust form should precede the diminutive Silurian representatives of the group. Whilst it is unlikely that genicular hoods could have developed from paired genicular spines, the opposite would be quite reasonable: the genicular hood of *P. undulatus* (Figs 3, 4, pp. 14, 15) is not unlike a pair of horse-blinkers (p. 90) and ventral elongation of these two parts of the hood could certainly result in paired spines. The process would be very similar to the production of paired spines in *Saetograptus* from a basic paired lappet structure in *M. ludensis*. *C. i. pacificus*, therefore, may be an offshoot of the main *innotatus* line of evolution.

*Climacograptus typicalis* Hall 1865

(Fig. 2, p. 12)

The *Amplexograptus*-like thecae are clearly exhibited by the specimen illustrated, as is the pronounced genicular process and its similarity to that of *C. i. jordaniensis*.

*Climacograptus nebula* (Toghill & Strachan 1970)

The best-preserved specimens of this species come not from Grieston Quarry where it was first described nor from the Lake District where one of us (J. E. H.) has recently collected it, but the Howgill Fells where it is extremely abundant in the upper *turriculatus* to *griestoniensis* Zones inclusive. Both the Lake District and Howgill Fells specimens display a pronounced geniculum, to a degree that convinces us (e.g. Hutt 1974) that the species should be referred to *Climacograptus* and not doubtfully to *Glyptograptus* as was done by its authors. Whether its origins lie with *Climacograptus* or *Glyptograptus* is uncertain, but there are certainly small species of *Climacograptus* (e.g. *C. simplex*) in the *sedgwickii* Zone which might lead directly to *C. nebula*.

Genus *PSEUDOCLIMACOGRAPTUS* Přibyl 1948Subgenus *PSEUDOCLIMACOGRAPTUS* Přibyl 1948*Pseudoclimacograptus (P.) orientalis* Obut & Sobolevskaya 1966

(Fig. 3, p. 14)

Although earlier recorded from the *cyphus* and *triangulatus* Zones by Obut & Sobolevskaya (1966, 1968) and from the 'gregarius' Zone of Dalarne by J. E. H. and R. B. R. (unpublished information; Fig. 3) we have recently been informed by N. Sennikov of Novosibirsk that he has recorded the species in association with *A. cf. acuminatus* in what he presumes to be the *acuminatus* Zone. Thus it is possible that a tenuous link existed between the latest (rare) Ordovician pseudoclimacograptids and those in the Silurian. The Swedish specimens are the only ones isolated from the matrix (Fig. 3) and it is clear that they should be referred to the subgenus *P. (Pseudoclimacograptus)* and not to *P. (Metaclimacograptus)*.

Subgenus *METACLIMACOGRAPTUS* Bulman & Rickards 1968*Pseudoclimacograptus (Metaclimacograptus)* sp.

(Fig. 3, p. 14)

A relatively robust species of metaclimacograptid has been identified by one of us (R. B. R.) from the *convolutus* Zone of Qusayba, Saudi Arabia. The species is very similar to *P. (M.) undulatus* in the angular median septum and in the presence of genicular hoods. However, the genicular hoods appear to be as equally developed ventrally as ventrolaterally whilst the rhabdosome is more robust (1.2 mm approximate dorsoventral width) and the thecae more widely spaced (13 in 10 mm distally).

Genus *AKIDOGRAPTUS* Davies 1929*Akidograptus ascensus* Davies 1929

(Fig. 7, p. 19)

Stein (1965) concluded that Bulman's (1933, 1936) interpretation of *A. ascensus*, in which he suggested loss or reduction of  $thr^2$ , was incorrect. Bulman himself



tends to agree with Stein (Bulman, personal communication), but we consider that the type specimens may well have some structure resembling a reduced *thr*<sup>2</sup>. Further work on three-dimensional or transparent material is required before the matter can be finally resolved. In any event there is no true uniserial portion, the thecal apertures alternating throughout, and the species is essentially a climacograptid with elongate proximal thecae. Other species are known, however (*A. giganteus* Yang 1964, and, indeed, *A. ascensus*, *sensu* Stein 1965), in which the distal thecae become 'dichograptid' in type, possibly implying the acquisition of diplograptid tendencies by a climacograptid stock.

Genus **GLYPTOGRAPTUS** Lapworth 1873

Subgenus **GLYPTOGRAPTUS** Lapworth 1873

***Glyptograptus (G.) persculptus*** (Salter 1875)

(Figs 8, p. 22, and 53; Pl. 2, fig. 4)

As has been partly shown by Davies (1929), there is considerable variation amongst the recorded specimens of *G. persculptus* from several well-known localities. Lake District specimens, for example, although certainly at the same horizon as the Welsh specimens, seem to be rather shorter and more slender; the Southern Uplands collections show again slight differences but in an essentially similar assemblage. Although much work needs to be done, we have singled out one form (Fig. 8a, specimen on right) because of its striking similarity to the distal thecae of *Rhaphidograptus toernquisti*. The dorsoventral width, appearance of the thecae, thecal spacing and general rhabdosomal proportions are closely similar, and it would be almost impossible to distinguish the distal thecae of the two species. In true profile, and with three-dimensional material, the thecae of *G. persculptus* s.l. have the supragenicular thecal walls inclined outwards at a slightly higher angle, whereas those on *R. toernquisti* are almost vertical.



FIG. 53. *Glyptograptus persculptus* (Salter), syntype SM A20413,  $\times 5$ , typical specimen from Pumpsaint, for contrast with the more slender specimens often referred to *G. persculptus* (Fig. 8, p. 22).

***Glyptograptus (G.) serratus barbatus*** Elles & Wood 1907

This subspecies is very similar indeed to '*Comograptus*' *comatus* Obut & Sobolevskaya (*in* Obut, Sobolevskaya & Merkuryeva 1968). The Anglesey specimens may

be slightly more robust, but have a similar thecal spacing. We agree with Elles & Wood in placing the form in the genus *Glyptograptus*, although it may eventually be shown to be specifically distinct from the coeval species *G. serratus serratus* Elles & Wood. Details of the proximal end and spinosity have not been fully established, but some of the more distal spines are certainly genicular in origin and may bifurcate, whilst at the extreme proximal end (Elles & Wood 1907: fig. 170b) there are at least a dozen slender spines some of which may depend from the sicular aperture (Rickards & Koren' 1974).

One of us (R. B. R.) has examined the types and other specimens of '*Comograptus* *comatus*'. Many of the spines are genicular in origin, and some bifurcate, whilst the sicular aperture almost certainly has a ring of pendant spines as in *G. (Pseudoglyptograptus) rhayaderensis* Rickards & Koren' (= *G. (P.)* sp. 3 of Rickards 1972) and *G. (P.) tabukensis* Rickards & Koren'. Some of the distal thecae in the type specimens of '*Comograptus* *comatus*' have a concave supragenicular wall suggesting that the species may be referable to *G. (Pseudoglyptograptus)*.

**'*Comograptus* *comatus*' Obut & Sobolevskaya 1968**

(Fig. 54)

Obut & Sobolevskaya (*in* Obut, Sobolevskaya & Merkuryeva 1968) point out that the main difference between this species and *G. s. barbatus* Elles & Wood is that the latter is more robust (up to 3.5 mm wide), longer (up to 50 mm) and with a slightly different thecal spacing (8-14 in 10 mm as against 10-12 in 10 mm in '*C. comatus*'). However, there is clearly considerable variation in the species of Elles & Wood (1901-18: pl. 30, figs 11a, b) and the above differences are easily accounted for by tectonic deformation.

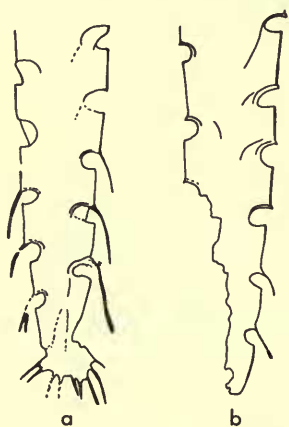


FIG. 54. a, '*Comograptus* *comatus*' after Obut & Sobolevskaya (1968). b, same, SM A79136, donated by Obut; both figures  $\times 5$ .

Genus **ORTHOGRAPTUS** Lapworth 1873

***Orthograptus mutabilis* Elles & Wood 1907**

(Fig. 12, p. 27)

*O. mutabilis* was suggested as a possible '*Dittograptus*' species by Obut & Sobolevskaya (*in* Obut, Sobolevskaya & Merkuryeva 1968), but that genus can

readily be accommodated in *Orthograptus* (Rickards 1970), the only distinctive feature of *D. fortuitus* worthy of comment being the slightly rounded nature of the apertural lip not unlike that seen in some dimorphograptids. In the British Silurian rather narrower forms than that figured by Elles & Wood (1907: pl. 29, figs 1a-c) are more common (1907: pl. 29, fig. 1d) and such specimens from the Lake District have thr<sup>1</sup> growing at first downwards in the manner normal for orthograptids. The specimens depicted by Elles & Wood as pl. 29, figs 1a-c resemble some continental petalograptids, and may be regarded at least as orthograptids with some petalograptid tendencies.

***Orthograptus insectiformis* (Nicholson 1869)**

(Fig. 12, p. 27)

It has recently been shown by Hutt (1974) and Rickards & Koren' (1974) that the type specimens of this species display pronounced virgellar division similar to that described by Hutt *et al.* (1970) in *Orthograptus* ? sp. and in *O. obuti* (Rickards & Koren' 1974). Paired apertural spines were first detected in the species by Churkin & Carter (1970) on North American specimens and confirmed by Hutt (1974) on Lake District specimens and Nicholson's type material. The actual spine bases have not been determined accurately, but on some they appear to be ventro-apertural.

***Orthograptus bellulus* Törnquist 1890**

(Fig. 12, p. 27)

Apertural spines were noted by Törnquist (1890) in his original description, a feature which has gone unnoticed by subsequent authors until detected on the Lake District material by Hutt (1974). The Howgill Fells specimens identified as *O. cf. insectiformis* by Rickards (1970) should probably be referred to *O. bellulus*: pyritized specimens do not usually show the thecal spines very clearly. In the type material the spine bases are positioned ventrolaterally.

***Orthograptus cyperoides* (Törnquist 1897)**

(Fig. 12, p. 27)

It has been noted by Hutt (1974) that *O. insectiformis* has always been identified from flattened material whereas Törnquist's (1897) species is almost always identified from specimens in relief. Two three-dimensional specimens from the Lake District were found to have very delicate thecal spines, and Hutt (1974) suggested that either they were only occasionally developed on the species, or they were rarely preserved. If the latter interpretation is correct then *O. cyperoides* may be a junior synonym of *O. insectiformis* (Nicholson 1869) which has an identical stratigraphic range and closely similar dimensions.

Genus **RHAPHIDOGRAPTUS** Bulman 1936[= *Metadimorphograptus* Přibyl 1948]***Rhaphidograptus toernquisti*** (Elles & Wood 1906)

(Fig. 8, p. 22 ; Pl. 1, figs 1-2 ; Pl. 2, fig. 1)

The species undoubtedly possesses delicate genicular hoods (Hutt 1974), a feature which whilst probably not of great classificatory importance does at least emphasize the extremely widespread occurrence of this structure, particularly amongst Llandovery graptoloids. The thecae are usually rather loosely described as climacograptid: in fact the thecal tubes are transversely expanded, that is narrow in a dorsoventral sense, the supragenicular wall is not quite vertical, and the infragenicular wall is almost glyptograptid. The species probably reflects the acquisition of near-climacograptid features by a glyptograptid ancestor such as *G. persculptus* s.l. (Fig. 8).

Genus **DIMORPHOGRAPTUS** Lapworth 1876[= *Bulmanograptus* Přibyl 1948]***Dimorphograptus* sp.**

(Fig. 10, p. 23)

The thecae exhibited by this species, although not yet fully understood, clearly demonstrate what has long been felt about *Dimorphograptus* species, namely that the thecal tube is not of simple orthograptid or dichograptid type. The free ventral wall of this form undoubtedly turns inward a little and the apertural margin appears to be slightly undulating. Other dimorphograptid species, such as those with 'isolated' thecae, may eventually be shown to have aberrant apertural margins.

Genus **ATAVOGRAPTUS** Rickards 1974

(Fig. 17, p. 37)

**GENERIC DIAGNOSIS.** Long slender rhabdosomes with gentle dorsal or flexuous curvature; thecae glyptograptid, elongate glyptograptid, or proto-monoclimacid; geniculation increases in later species; sacula short in earlier forms becoming longer (up to 3 mm) in later species; two species biform with elongate glyptograptid thecae distally and proto-monoclimacid thecae proximally.

**OCCURRENCE.** *Persculptus* to *magnus* Zones.

**TYPE SPECIES.** *Atavograptus atavus* (Jones 1909); Pl. 4, fig. 4; Pl. 6, fig. 1.

**SPECIES.** *A. atavus* (Jones), *A. ceryx* (Rickards & Hutt), *A. strachani* (Hutt & Rickards), *A. praestrachani* sp. nov., *A. gracilis* (Hutt), *A. renaudi* (Philipot).

***Atavograptus praestrachani* sp. nov.**

(Fig. 17, p. 37)

1970 *Monograptus* sp. 1; Hutt & Rickards: 75; figs 3c, d.

**HOLOTYPE.** The specimen figured Hutt & Rickards (1970: fig. 3c), specimen number A 60415 (Sedgwick Museum) from Keisley (National Grid ref. NY 71382379).



**DIAGNOSIS.** Rhabdosome dorsally curved with a proximal dorsoventral width of 0.25 mm (low relief) increasing to 0.90 mm distally; proximal thecal spacing 9–10 in 10 mm and distally down to 7 in 10 mm; proximal thecae *strachani*-like with sharp geniculum, distal thecae *atavus*-like, flowing geniculum and apertures slightly everted; change from proximal to distal type gradual; sicula 3 mm long reaching to just above the level of the aperture of th1.

**REMARKS.** Nothing further is added to the observations of Hutt & Rickards (1970), but the form's evolutionary position is now considered sufficiently well documented to justify its erection as a new species: morphologically and stratigraphically it is exactly intermediate between *A. atavus* and *A. strachani*.

Genus **PRIBYLOGRAPTUS** Obut & Sobolevskaya 1966,  
emend. Rickards (in press)

**EMENDED DIAGNOSIS.** Rhabdosome usually long and slender with flexuous curvature, but in one species more robust and straight, and in one with stiff curvature proximally. Sicula known in only one species where it is small reaching to about the aperture of th1. Thecae long, slender, usually inclined at less than 20 degrees to the axis of the rhabdosome, and with *pronounced* introversion of the apertural region which may also be furnished with a pair of lateral horns directed dorso-laterally, and overhung by a geniculum and perhaps with a genicular hood.

**TYPE SPECIES.** *Monograptus incommodus* Törnquist 1899.

Genus **CORONOGRAPTUS** Obut & Sobolevskaya (*in Obut et al.*) 1968,  
emend. Rickards (in press)

**EMENDED DIAGNOSIS.** Rhabdosomes mostly quite short, up to 40 mm, relatively robust with dorsal curvature varying from stiff to horseshoe-shaped. Sicula in early forms about 2 mm, but up to 12 mm in later species. Thecae relatively long, usually overlapping at least half the ventral wall, with a *rounded* geniculum pronounced in some species; thecal apertures even or slightly everted, and rarely isolate growing out over the geniculum and obscuring it.

**TYPE SPECIES.** *Monograptus gregarius* Lapworth 1876.

**REMARKS.** In addition to the species discussed above, p. 41, *M. leei* Hsü and *M. sp.* Hutt (1975) should probably also be included here: the latter shows some features intermediate between *Atavograptus* and *Coronograptus*.

Genus **LAGAROGRAPTUS** Obut & Sobolevskaya (*in Obut et al.*) 1968,  
emend. Rickards (in press)

**EMENDED DIAGNOSIS.** Rhabdosome with moderate dorsal curvature, relatively slim and parallel-sided. Sicula long but reaching at most to just above the aperture of th1; sicular aperture asymmetrical as in *C. gregarius*. Thecae long, slender, overlapping half to more than three-quarters of ventral wall; thecal apertures slightly everted, with semicircular excavation and pronounced overhanging

geniculum which may have genicular hood; striking *ventral apertural* process of triangular shape composed of fusellar tissue.

TYPE SPECIES. *Lagarograptus inexpeditus* Obut & Sobolevskaya (*in Obut et al.*) 1968.

REMARKS. The fusellar structure of the ventral apertural process has recently been established by one of us (R. B. R.) on Saudi Arabian specimens referable to *L. cf. tenuis* (Portlock), and there is a suggestion of fusellar growth bands on the type specimens from Norilsk. The genicular hood may possibly also be composed of fusellar tissue.

Genus **MONOGRAPTUS** Geinitz 1852, emend.

***Monograptus sudburiae*** Hutt 1974

(Figs 17, p. 37, and 19, p. 43)

1958 *Monograptus revolutus* C; Sudbury: 536, textfig. 26c.

Hutt's (1974) species is the type of a newly-defined group of biform monograptids in which the proximal thecae display retroverted hooks and the distal thecae strong introversion. The change is gradual throughout the rhabdosome. The most proximal thecae have a dorsoventral width of less than 0.20 mm, and a thecal spacing of  $7\frac{1}{2}$  in 10 mm, and no thecal overlap; distally the dorsoventral width is 0.50–0.60 mm (in relief), the thecal spacing 10–10½ in 10 mm and the thecal overlap about a half. Just before the maximum thecal overlap develops, coinciding with a tightening of the rhabdosome's curvature, the thecae become introverted. *M. revolutus* Kurck 1882 displays the same basic structure but has a more robust rhabdosome and a more restricted occurrence (*cyphus* Zone).

***Monograptus delicatulus*** Elles & Wood 1913

(Fig. 38, p. 73)

Material from the Soviet Union recently isolated seems to fit Elles & Wood's (1913) description very well but in addition displays very long, slender, ventrolaterally-directed spines. The thickened dorsal lip of the hook depends proximally between the spines, which may have evolved from an original paired horn structure. The sicula of the Russian specimens has a pronounced curvature.

***Monograptus walkerae*** nom. nov.

1958 *Monograptus toernquisti* sp. nov.; Sudbury: 514.

Stein (1965) has pointed out that Sudbury's (1958) species name is a junior homonym of *M. toernquisti* (Eisel 1912), and we herein propose the new name *M. walkerae* to replace *M. toernquisti*, *sensu* Sudbury (née Walker). Similarly *M. toernquisti elongatus* Sudbury is a junior homonym of *M. elongatus* Törnquist 1899, and we herein propose the name *M. walkerae rheidolensis* as a new name for Sudbury's subspecies.

***Monograptus* sp. A**

(Fig. 25, p. 56)

The single specimen from the *gregarius* Zone of Dobb's Linn, probably *magnus* level, was collected by Dr H. Jaeger on the 1969 Ludlow Research Group excursion, and is the earliest known *Monograptus* s.s. The length of the rhabdosome is 67 mm and displays conspicuous gentle dorsal curvature throughout: the dorsoventral width (almost flattened) is 0.4–0.5 mm at the level of th1 and th2, 0.7–0.8 at th20–24, and distally achieves 0.90 mm. The sicula has a length of about 1.3 mm, its apex reaching to the top of th1. Thecal spacing at the proximal end is 10 in 10 mm falling to 9–10 in 10 mm more distally. Thecal overlap is not clear but probably small. The thecae are uniform except that the distal thecal hooks exhibit dorsal wall retroversion to the extent that the hook looks almost spinose (Fig. 25, p. 56). The ventral wall of the theca seems not to participate in the hook, which is therefore best described as a very pronounced hood. Although growth lines are difficult to discern they have been detected on the hood of th60, for example, and a few other thecae, indicating that the hood is composed of fusellar tissue. *M.* cf. *concinus* occurs on the same slab as *M.* sp. A, and Toghill records *M. concinns* from the top of the *gregarius* Zone in Dobb's Linn.

***Monograptus turriculatus* Barrande 1850**

(Fig. 36, p. 71)

Hutt (1975) has recently recorded bifurcating apertural spines in this species, thus supporting the preliminary observations of Bulman & Rickards (*in* Bulman 1970), although it should be emphasized that the actual detailed structure of the thecae is not yet known. We support earlier suggestions that in Britain, at least, *M. turriculatus minor* Bouček cannot be distinguished. Mr L. Sherwin has informed us of a species superficially similar to *M. turriculatus* from the Cotton Beds of the Forbes District in Australia, which differs from the latter mainly in having a shorter sicula and a lower conical spiral so that specimens are most commonly preserved on the bedding plane in the form of a plane spiral.

**Genus *PRISTIOGRAPTUS* Jaekel 1889*****Pristiograptus* spp. 1 and 2**

(Figs 30, p. 65, and 55)

Two unnamed species have been described by Hutt (1974) from the *magnus* and *argenteus* Zones of the Lake District, sp. 1 occurring only in the *magnus* Zone, and sp. 2 in both zones. *P.* sp. 1 has a sicula 1.3–1.4 mm long, a thecal spacing of 10 in 10 mm proximally and 11½ in 10 mm distally, and a dorsoventral width of 0.20 mm at the level of th1 increasing to 0.5 mm at th9 (flattened). The thecal apertures are horizontal, even fractionally introverted, and the appearance as a whole is of a form intermediate between *A. atavus* and later *pristiograptids*.

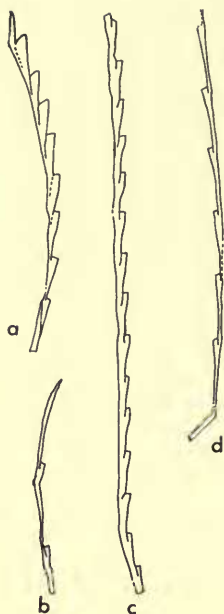


FIG. 55. Early pristiograptids: a, *P. sp.*, LU 57771, *magnus* Zone, Skelgill, Lake District; b, *P. fragilis* (Rickards), LU 57589, *acinaces* Zone, Yewdale Beck, Lake District; c, *P. sp.*, LU 57772, *magnus* Zone, Skelgill, Lake District; d, *P. fragilis* (Rickards), LU 57587, *magnus* Zone, Yewdale Beck, Lake District. All figures  $\times 5$ .

The proximal end of *P. sp. 2* is not known but the fragments have a dorsoventral width of 0.30–0.35 mm and a thecal spacing of 10 in 10 mm. Overlap is one-eighth and the angle of inclination a little over 10 degrees.

#### VIII. IN RETROSPECT

A general survey of the main features in the evolution of Siluro-Devonian graptoloids is indicated in Fig. 1, p. 7. To be noted is the rapid diversification of the Silurian graptolites into many lineages during the early and middle Llandovery following an interval near the end of the Ordovician during which so many lineages of graptolites died out that they came close to becoming totally extinct. Early Silurian diversification appears to have reached its peak in about the *cyphus* Zone. Relatively gradual reductions took place in most lineages throughout the remainder of the Llandovery, a trend which culminated in the extinction or near-extinction of many graptolite stocks in the latest Llandovery–early Wenlock interval. At that time, the genera *Averianowograptus*, *Barrandeograptus*, *Damosiograptus*, *Diversograptus*, *Oktavites*, *Spirograptus*, *Streptograptus*, *Uralograptus* and the retiolitids (*Retiolites*, *Stomatograptus*) became extinct. The stocks included herein as late Llandovery ‘cyrtograptids’ became extinct or nearly so during the *riccartonensis* Zone. They were replaced in strata above the *riccartonensis* Zone by one or more new ‘cyrtograptid’ lineages that probably developed from ancestors other than the late Llandovery ‘cyrtograptids’. In addition, the monoclimalacids and monograptids s.s. were reduced in diversity in the early Wenlock.



The latest Llandovery-early Wenlock extinctions and reductions in diversity were followed during the remainder of the Wenlock by three essentially stable, widely-found stocks, the pristiograptids, the monoclimacids and the monograptids s.s. Certain short-lived stocks such as the *flexilis* group developed from the monograptids, and a number of species arose among the pristiograptids. The latter part of the Wenlock is typified by the appearance of members of the Subfamily Plectograptinae (including *Gothograptus* and *Plectograptus*) and the lineages of post-*riccartonensis* Zone 'cyrtograptids'.

A relatively sudden 'burst' in diversity or marked development of several new lineages characterizes the early Ludlow. The newly-appearing lineages probably were derived from the pristiograptid lineage. Representatives of *Bohemograptus*, *Colonograptus*, *Neodiversograptus* and *Saetograptus* as well as members of the *uncinatus* group typify the early Ludlow radiation. These and the other stocks that developed during the early Ludlow 'burst' were relatively short-lived as their numbers dwindled markedly in the latter part of the Ludlow.

At least three new stocks (the *formosus* group, the *transgrediens* group and the earliest members of the *hercynicus-yukonensis* lineage) appeared in the latest Ludlow-early Pridoli. Members of the *hercynicus-yukonensis* lineage survived into the early Devonian and probably included the youngest and last of the graptolites. The appearance of *M. uniformis* in the *hercynicus-yukonensis* lineage as well as the appearance of certain other taxa such as *Abiesgraptus* (developed from *Linograptus*) denote the base of the Devonian.

The general evolutionary history is thus one of marked radiation into many stocks in the early part of the Llandovery followed by reduction in most lineages, culminating in marked extinctions and reductions in the early Wenlock *riccartonensis* Zone. That event was followed by stability in most stocks and appearance of only a few new lineages until the early Ludlow when a relatively small but marked 'burst' in radiation occurred. Thereafter the number of graptolite stocks diminished although some replacements of those that became extinct by new stocks did take place up until the latter part of the early Devonian.

A review of the general trends in rhabdosome and thecal characteristics observed among the Siluro-Devonian graptolites indicates that many of these features appear in several different lineages. Acquisition of features such as thecal hooks and spines or spiral rhabdosome form by members of different lineages suggests that the features had an adaptive significance and were of importance not only in modes and places of life of the colonies but also in colony survival. For example, protection of the apertural region appears to have been important for colonies of many lineages. It was achieved through thecal introversion and retroversion as well as spines and probably hooks and hoods.

Analysis of evolutionary patterns among the Siluro-Devonian graptolites indicates a contrast in mode of appearance of founder species of new lineages. Some stocks, such as the rastritids, demirastritids, neodiversograptids and saetograptids, appear in the stratigraphic record relatively suddenly as morphologically clearly-defined taxa. These and similar stocks were relatively short-lived, in general. In contrast with them, the original or founding species of long-lived stocks such as

the pristiograptids, monoclimacids and monograptids are not clearly distinguishable. In the case of such stocks, the species that are possible candidates as their initial members are closely similar morphologically to species in the lineage from which they originated. This relationship is consistent with the processes of speciation described by Mayr (1963), among others, in which new species are visualized as developing as local populations from a parental population or group of local populations by some form of isolation. In the speciation process as discussed by Mayr, a newly-developed daughter species may be little different morphologically from its parent and yet, when the phyletic history of whole lineages is established, such a daughter may be recognized as the initial member of a new lineage. The available record of the origin of some Siluro-Devonian graptolite lineages, such as the pristiograptids and monoclimacids, appears to be at least consistent with if not fully corroborative of such a theoretical pattern of speciation leading to the origin of a new lineage.

The contrasting patterns in evolutionary development may reflect differences in the availability of potential niches for graptolite species, particularly those with new modes or places of life. The lineages that arose with founder species showing little morphological difference from their parental species appeared at times when many different lineages were in existence and probably potential niches were fully or almost fully exploited. The lineages in which the initial members appear in the stratigraphic record as new taxa, relatively clearly morphologically different, developed at times when few lineages were present. Many potential niches appear to have been available at times when few lineages were in existence. The widespread availability of potential niches appears, from the evolutionary history of the Siluro-Devonian graptolites, to have been a major factor in the marked adaptive radiations or 'bursts' in taxonomic diversity.

Although certain aspects of the evolutionary history suggested herein may, and probably will, be modified through future researches, the basic patterns appear to be relatively well founded. Initial versions of Fig. 1 (p. 7) were developed in 1966-67. They have been tested through vigorous and detailed stratigraphic collecting by the authors over seven years in different areas in the world. In addition, existing collections from many parts of the Siluro-Devonian succession in several areas of the world have been examined. These critical studies have not substantially modified most of the basic aspects of the initially-recognized lineages and their relationships, although many new details have been discovered and used to refine the initial versions of Fig. 1 and produce the version herein. Future work will doubtless pinpoint phyletic intermediates along some lineages and suggest range extensions and expansions of others. Despite these expected and, indeed, hoped-for modifications, the basic patterns indicated provide a tool that stratigraphers interested in dating Silurian-early Devonian rocks using graptolites may use. The phyletic developments indicated in Fig. 1 may also be used to refine understanding of the zonal sequence because the appearance of a new lineage is a unique event which may be considered an appropriate marker of a zone boundary, or at least a point in time.

Evolutionary development as indicated in Fig. 1 and discussed in the text may be analysed from different points of view, which include, in addition to increasing comprehension of the patterns of organic evolution, the establishing of possible relationships between adaptive radiation and availability of potential niches, making age determinations, and refining zone boundaries.

## IX. REFERENCES

- AVERIANOW, B. 1929. Graptoloidea der obersilurischen Schiefer aus Ost-Turkestan. *Izv. geol. Kom.*, St Petersburg, **48** (5) : 101-124.
- BASSETT, M. G. & RICKARDS, R. B. 1971. Notes on Silurian stratigraphy and correlation in the Oslo district. *Norsk geol. Tidsskr.*, Oslo, **51** : 247-260.
- BERRY, W. B. N. 1969. Some aspects of monograptid graptolite evolution. *Abstr. Progm. geol. Soc. Am.* **1969** (7) : 12-13.
- & BOUCOT, A. J. 1972. Correlation of the South American Silurian rocks. *Spec. Pap. geol. Soc. Am.*, New York, **133**, 59 pp.
- & MURPHY, M. A. 1972. Early Devonian Graptolites from the Rabbit Hill Limestone in Nevada. *J. Paleont.*, Chicago, **46** : 261-265.
- BOUČEK, B. 1933. Monographie der obersilurischen Graptolithen aus der Familie Cyrtograptidae. *Pr. geol.-paleont. úst. Karlov. Univ.*, Prague, **1**. 84 pp., 6 pls.
- & MÜNCH, A. 1944. Retioliti střeoevropského Llandovery a spodního Wenlocku. *Rozpr. české Akad. Věd Umění*, Prague, **53** (41) : 1-50. Die Retioliten des mitteleuropäischen Llandovery und unteren Wenlock. *Bull. int. Acad. tchèque Sci.*, Prague, **44** : 527-580.
- 1952. Retioliti střeoevropského surnchniho Wenlocku a Ludlowu. *Sb. Ustřed. Ust. Geol.*, Prague, **19** : 1-54 and 104-151.
- & PŘIBYL, A. 1941. O rodu *Petalolithus* Suess z českého siluru. *Rozpr. české Akad. Věd Umění*, Prague, **51** (11) : 1-17.
- 1943. O českých monograptech z podrodu *Streptograptus* Yin. *Rozpr. české Akad. Věd Umění*, Prague, **52** (1) : 1-23. Über böhmische Monograpten aus der Untergattung *Streptograptus* Yin. *Bull. int. Acad. tchèque Sci.*, Prague, **43** : 1-23.
- 1952. On some slender species of the genus *Monograptus* Geinitz, especially of the subgenera *Mediograptus* and *Globosograptus*. *Bull. int. Acad. tchèque Sci.*, Prague, **52** : 185-216.
- 1954. Contribution to our Knowledge of the *Cyrtograptids* from the Silurian of Bohemia and on their Stratigraphical Importance. *Bull. int. Acad. tchèque Sci.*, Prague, **53** : 177-201.
- BULMAN, O. M. B. 1929. The genotypes of the genera of graptolites. *Ann. Mag. nat. Hist.*, London, (10) **4** : 169-185.
- 1932. On the graptolites prepared by Holm, 4. New species of *Didymograptus* and *Dicellograptus* from Öland, with remarks on the development of *Dicellograptus*. *Ark. Zool.*, Stockholm, **24A** (9) : 15-21.
- 1933. Notes on the Evolution and Morphology of certain Graptoloidea. *Ark. Zool.*, Stockholm, **24A** (13) : 1-37.
- 1936. *Rhaphidograptus*, a new graptolite genus. *Geol. Mag.*, London, **73** : 19-26.
- 1951. Notes on thecal variation in *Monograptus*. *Geol. Mag.*, London, **88** : 316-328.
- 1955. Graptolithina, with sections on Enteropneusta and Pterobranchia. In MOORE, R. C. (ed.). *Treatise on Invertebrate Paleontology*, V. xvii + 101 pp., illustr. Kansas.
- 1958. The sequence of graptolite faunas. *Palaeontology*, London, **1** : 159-173.
- 1963. The evolution and classification of the graptoloidea. *Q. Jl. geol. Soc. Lond.* **119** : 401-418.



- BULMAN, O. M. B. 1965. Giant rhabdosomes of *Monograptus* cf. *flemingii* (Salter). *Proc. geol. Soc.*, London, **1624** : 99-102.
- 1970. Graptolithina, with sections on Enteropneusta and Pterobranchia. In TEICHERT, C. (ed.). *Treatise on Invertebrate Paleontology*, V, 2nd edition. xxxii + 163 pp., illustr. Kansas.
- & RICKARDS, R. B. 1968. Some new diplograptids from the Llandovery of Britain and Scandinavia. *Palaeontology*, London, **11** : 1-15.
- BURGESS, I. C., RICKARDS, R. B. & STRACHAN, I. 1970. The Silurian strata of the Cross Fell area. *Bull. geol. Surv. Gt Br.*, London, **32** : 167-182.
- CHURKIN, M., jr 1963. Graptolite beds in thrust plates of Central Idaho and their correlation with sequences in Nevada. *Bull. Am. Ass. Petrol. Geol.*, Chicago, **47** : 1611-1623.
- & CARTER, C. 1970. Early Silurian graptolites from south eastern Alaska and their correlation with graptolite sequences in North America and the Arctic. *Prof. Pap. U.S. geol. Surv.*, Washington, **653** : 1-51.
- , JAEGER, H. & EBERLEIN, G. D. 1970. Lower Devonian graptolites from southeastern Alaska. *Lethaia*, Oslo, **3** : 183-202.
- & KAY, M. 1967. Graptolite-bearing Ordovician Siliceous and Volcanic Rocks, Northern Independence Range, Nevada. *Bull. geol. Soc. Am.*, New York, **78** : 651-668.
- COCKS, L. R. M., HOLLAND, C. H., RICKARDS, R. B. & STRACHAN, I. 1971. A correlation of Silurian rocks in the British Isles. *Q. Jl geol. Soc. Lond.* **127** : 103-136.
- DAVIES, K. A. 1929. Notes on the graptolite faunas of the Upper Ordovician and Lower Silurian. *Geol. Mag.*, London, **66** : 1-27.
- EISEL, R. 1912. Über zonenweise Entwicklung der Rastriten und Demirastriten. *Jber. Ges. Freunden Naturw. Gera* **53/54** : 27-43.
- ELLES, G. L. 1922. The graptolite faunas of the British Isles. A study in evolution. *Proc. Geol. Ass.*, London, **33** : 168-200.
- & WOOD, E. M. R. 1901-18. A monograph of British Graptolites. (Ed. by C. Lapworth.) *Palaeontogr. Soc. (Monogr.)*, London. clxxi + 539 pp.
- GEORGE, T. N. 1962. The concept of homeomorphy. *Proc. Geol. Ass.*, London, **73** : 9-64.
- HOLLAND, C. H., RICKARDS, R. B. & WARREN, P. T. 1969. The Wenlock graptolites of the Ludlow district, Shropshire, and their stratigraphical significance. *Palaeontology*, London, **12** : 663-683.
- HOLM, G. 1890. Gotlands Graptoliter. *Bih. K. svenska VetenskAkad. Handl.*, Stockholm, **16** (4) : 1-34.
- HOPKINSON, J. 1869. On British graptolites. *J. Quekett microsc. Club*, London, **1** : 151-166.
- HSÜ S. C. 1934. The graptolites of the Lower Yangtze Valley. *Monogr. natn. Res. Inst. Geol. Shanghai* (A) **4** : 1-106.
- HUNDT, R. 1942. Beiträge zur Kenntnis des Mitteldeutschen Graptolithenmeeres. *Beitr. Geol. Thür.*, Jena, **6** : 205-231.
- HUTT, J. E. 1968. A redescription of the Llandovery monograptid "*Graptolithus*" *tenuis*, Portlock, 1843. *Geol. Mag.*, London, **105** : 251-255.
- 1969. The development of the Ludlovian graptolite *Saetograptus varians*. *Lethaia*, Oslo, **2** : 361-368.
- 1974. A new group of Llandovery biform monograptids. In RICKARDS, R. B., JACKSON, D. E. & HUGHES, C. P. (eds). Graptolite studies in honour of O.M.B. Bulman. *Spec. Pap. Palaeont.*, London, **13** : 189-203.
- 1975. The Llandovery graptolites of the English Lake District. Part 2. *Palaeontogr. Soc. (Monogr.)*, London : 57-137.
- & RICKARDS, R. B. 1970. The evolution of the earliest Llandovery monograptids. *Geol. Mag.*, London, **107** : 67-77.
- & BERRY, W. B. N. 1972. Some Major Elements in the Evolution of Silurian and Devonian Graptoloids. *24th Int. geol. Congr.* (Montreal), sec. 7 (Palaeontology) : 163-173.
- & SKEVINGTON, D. 1970. Isolated Silurian graptolites from the Bolterup and Klubbudden stages of Dalarna, Sweden. *Geologica Paleont.*, Marburg, **4** : 1-23.



- HUXLEY, J. S. 1958. Evolutionary processes and taxonomy. *Uppsala Univ. Arsskr.* **6** : 21-39.
- JAANUSSON, V. 1960. Graptoloids from the Ontikan and Viruan (Ordov.) limestones of Estonia and Sweden. *Bull. geol. Instn Univ. Upsala* **38** : 289-366.
- 1973. Morphological discontinuities in the evolution of graptolite colonies. In BOARDMAN, R. S. *et al.* (eds). *Animal colonies : their development and function through time* : 515-521. Stroudsburg, Penn.
- JACKSON, D. E. & ETHERINGTON, J. R. 1969. New Silurian cyrtograptid graptolites from northwestern Canada and northern Greenland. *J. Paleont.*, Chicago, **43** : 1114-1121.
- & LENZ, A. C. 1962. Zonation of Ordovician and Silurian graptolites of northern Yukon, Canada. *Bull. Am. Ass. Petrol. Geol.*, Chicago, **46** : 30-45.
- — 1969. Latest Silurian graptolites from Porcupine River, Yukon Territory. *Bull. geol. Surv. Can.*, Ottawa, **182** : 17-29.
- — 1972. Monograptids from the Upper Silurian and Lower Devonian of Yukon Territory, Canada. *Palaeontology*, London, **15** : 579-597.
- JAEGER, H. 1959. Graptolithen und Stratigraphie des jüngsten Thüringer Silurs. *Abh. dt. Akad. Wiss. Berl.*, Kl. Chem. Geol. Biol. **1959** (2) : 1-197.
- 1970. Remarks on the stratigraphy and morphology of Praguian and probably younger monograptids. *Lethaia*, Oslo, **3** : 173-182.
- JONES, W. D. V. & RICKARDS, R. B. 1967. *Diplograptus penna* Hopkinson 1869, and its bearing on vesicular structures. *Palaeont. Z.*, Stuttgart, **41** (3/4) : 173-185.
- KIRK, N. 1973. Some thoughts on the construction and functioning of the rhabdosome in the Retiolitidae. *Publs Dep. Geol. Univ. Coll. Wales, Aberystwyth*, **3** : 1-26.
- KOREN', T. N. 1962. Novyi siluriiskii rod *Uralograptus*. *Paleont. Zh.*, Moscow, **1962** (3) : 137-138. [In Russian.]
- 1968. Novye rannesiluriiskie graptolit'y yuzhnogo Urala. *Paleont. Zh.*, Moscow, **1968** (4) : 101-103. [In Russian.]
- 1971. The zones of *Monograptus hercynicus* and *Monograptus falcarius* in Pai-Khoi. *Lethaia*, Oslo, **4** : 235-248.
- 1973. The Silurian and Lower Devonian graptolite-bearing strata in the USSR (a review). *Geol. Mag.*, London, **110** : 1-17.
- KURCK, C. 1882. Några nya Graptolitarter från Skåne. *Geol. Förel. Stockh. Förel.* **6** : 294-304.
- LAPWORTH, C. 1876. On Scottish Monograptidae. *Geol. Mag.*, London, (2) **3** : 308-321, 350-360, 499-507, 541-552.
- LEE C. K. 1963. Some Middle Ordovician graptolites from Guizhan. *Acta palaeont. sin.*, Peking, **11** : 554-578.
- LEGRAND, P. 1970. Les couches à *Diplograptus* du Tassili de Tarit (Ahnet, Sahara algérien). *Bull. Soc. Hist. nat. Afr. N.*, Algiers, **6** : 3-58.
- LENZ, A. C. & JACKSON, D. E. 1971. Latest Silurian (Pridolian) and Early Devonian *Monograptus* of Northwestern Canada. In Contributions to Canadian Paleontology. *Bull. geol. Surv. Can.*, Ottawa, **192** : 1-26.
- LEVINA, E. F. 1928. Graptolity iz Ak-Tengi v Turkestanskom Khrebte. *Acta Univ. Asiae mediae*, Tashkent, ser. VIIa (Geol.) **5** : 1-18. [In Russian with English summary.]
- MAYR, E. 1963. *Animal species and evolution*. 797 pp. Cambridge, Mass.
- MU A. T. & CHEN X. 1962. *Sinodiversograptus multibrachiatus* gen. et sp. nov. and its developmental stages. *Acta palaeont. sin.*, Peking, **10** : 143-154.
- & LEE C. K. 1958. Scandent graptolites from the Ningkuo Shale of the Kiangschan-Chanshan area, Western Chekiang. *Acta palaeont. sin.*, Peking, **6** : 391-427.
- MÜNCH, A. 1952. Die Graptolithen aus dem anstehenden Gotlandium Deutschlands und der Tschechoslowakei. *Geologica, Berl.* **7** : 1-197.
- NICHOLSON, H. A. 1869. On some new species of graptolites. *Ann. Mag. nat. Hist.*, London, (4) **4** : 231-242.
- OBUT, A. M. 1949. *Polevoi atlas rukovodyashchikh graptolitov verkhnego silura Kirgizskoi SSR*. 56 pp. Frunze, Izd. Kirgiz. Fil. Akad. Nauk SSSR. [In Russian.]

- OBUT, A. M. 1965. Graptolity silura omulevskikh gor (Bassein reki Kolymiz). In: *Stratigrafiya paleontologiya paleozoya aziatskoi chasty SSSR*: 33-46. Moscow, Akad. Nauk SSSR (Sibirsk. otdel. Inst. Geol. Geofiz.). [In Russian.]
- & SOBOLEVSKAYA, R. F. 1966. *Graptolity rannego silura v kazakhstane*. 56 pp. Moscow, Akad. Nauk SSSR (Sibirsk. otdel. Inst. Geol. Geofiz.). [In Russian.]
- 1967. In OBUT, A. M., SOBOLEVSKAYA, R. F. & NIKOLAEV, A. A., *Graptolityi stratigrafiya nizhnego silura okrainnykh podnyatti Kolym'skogo Massiva (Severo Vostok SSSR)*. 162 pp. Moscow, Akad. Nauk SSSR (Sibirsk. otdel. Inst. Geol. Geofiz.). [In Russian.]
- & BONDAREV, V. E. 1965. *Graptolity silura Taimyra*. 120 pp. Moscow, Akad. Nauk SSSR. [In Russian.]
- & MERKURYEVA, A. P. 1968. *Graptolity llandovery v kernakh burovykh skvazhin noryl'skogo rayona*. 136 pp. Moscow, Akad. Nauk SSSR (Sibirsk. otdel. Inst. Geol. Geofiz.). [In Russian.]
- PACKHAM, G. H. 1962. Some diplograptids from the British Lower Silurian. *Palaeontology*, London, **5**: 498-526.
- PALMER, D. 1971. The Ludlow graptolites *Neodiversograptus nilsoni* and *Cucullograptus (Lobograptus) progenitor*. *Lethaia*, Oslo, **4**: 357-384.
- PRIBYL, A. 1941. *Pernerograptus* nov. gen. und seine Vertreter aus dem böhmischen und ausländischen Silur. *Mém. Soc. r. Sci. Bohême*, Prague, **1941**: 1-18.
- 1945. The Middle-European monograptids of the genus *Spirograptus* Gürich. *Bull. int. Acad. tchéque Sci.*, Prague, **45**: 185-231. O středoevropských monograptech z rodu *Spirograptus* Gürich. *Rozpr. české Akad. Věd Umění*, Prague, **54** (19): 1-45.
- 1947. Classification of the genus *Climacograptus* Hall, 1865. *Bull. int. Acad. tchéque Sci.*, Prague, **48**: 17-28.
- 1948. Bibliographic Index of Bohemian Silurian Graptolites. *Knih. st. geol. Ust. čsl. Repub.*, Prague, **22**: 1-96.
- & MÜNCH, A. 1942. Revise středoevropských zástupců rodu *Demirastrites* Eisel. *Rozpr. české Akad. Věd Umění*, Prague, **51** (31): 1-30.
- RICKARDS, R. B. 1963. *The Silurian strata of the Howgill Fells*. Unpublished Ph.D. Thesis, University of Hull.
- 1965. New Silurian graptolites from the Howgill Fells (Northern England). *Palaeontology*, London, **8**: 247-271.
- 1967. The Wenlock and Ludlow succession in the Howgill Fells (north-west Yorkshire and Westmorland). *Q. Jl geol. Soc. Lond.* **123**: 215-251.
- 1968. The thecal structure of *Monoclimacis galaensis*. *Lethaia*, Oslo, **1**: 303-309.
- 1969. Wenlock graptolite zones in the English Lake District. *Proc. geol. Soc.*, London, **1654**: 61-65.
- 1970. The Llandovery (Silurian) graptolites of the Howgill Fells, Northern England. *Palaeontogr. Soc. (Monogr.)*, London: 1-108.
- 1972. *Climacograptus scalaris* (Hisinger) and the Subgenus *Glyptograptus (Pseudoglyptograptus)*. *Geol. Förf. Stockh. Förh.* **94**: 271-280.
- 1973. Bipolar monograptids and the Silurian genus *Diversograptus* Manck. *Palaeont. Z.*, Stuttgart, **47** (3/4): 175-187.
- (in press). *Classification of Monograptus: a redefinition of some Llandovery graptolite genera*. 2nd Soviet Graptolite Colloquium (Tallin, 1973).
- & HUTT, J. E. 1970. The earliest monograptid. *Proc. geol. Soc.*, London, **1663**: 115-119.
- & IORDAN, M. 1975. Rumanian graptolites from boreholes on the Moesian Platform. *Geol. Mag.*, London, **112**: 241-255.
- & KOREN', T. N. 1974. Virgellar meshworks and sicular spinosity in Llandovery graptoloids. *Geol. Mag.*, London, **111**: 193-272.
- & RUSHTON, A. W. A. 1968. The thecal form of some slender Llandovery *Monograptus*. *Geol. Mag.*, London, **105**: 264-274.

- RICKARDS, R. B. & SMYTH, W. R. 1968. The Silurian graptolites of Mayo and Galway. *Scient. Proc. R. Dubl. Soc.* A **3**: 129-134.
- RIVA, J. 1969. Middle and Upper Ordovician graptolite faunas of St. Lawrence lowlands of Quebec, and of Anticosti Island. In: KAY, M. (ed.). North Atlantic - Geology and Continental Drift. *Mem. Am. Assoc. Petrol. Geol.*, Tulsa, **12**: 513-556.
- ROSS, R. J. & BERRY, W. B. N. 1963. Ordovician graptolites of the Basin Ranges in California, Nevada, Utah and Idaho. *Bull. U.S. geol. Surv.*, Washington, **1134**: 1-177.
- RUEDEMANN, R. 1947. Graptolites of North America. *Mem. geol. Soc. Am.*, Washington, **19**: i-x, 1-652.
- SCHAUER, M. 1967. Biostratigraphie und Taxonomie von *Rastrites* (Graptolithina) aus dem anstehenden Silur Ostthüringens des Vogtlandes. *Freiberger ForschHft.*, Berlin, C **213**: 171-199.
- STEIN, V. 1965. Stratigraphische und paläontologische Untersuchungen im Silur des Frankenwaldes. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **121**: 111-200.
- STRACHAN, I. 1952. On the development of *Diversograptus* Manck. *Geol. Mag.*, London, **89**: 365-368.
- 1971. A synoptic supplement to "A Monograph of British Graptolites by Miss G. L. Elles and Miss E. M. R. Wood". *Palaeontogr. Soc. (Monogr.)*, London: 1-130.
- SUDBURY, M. 1958. Triangulate monograptids from the *Monograptus gregarius* Zone (lower Llandovery) of the Rheidol Gorge (Cardiganshire). *Phil. Trans. R. Soc.*, London, B **241**: 485-555.
- TELLER, L. 1964. Graptolite fauna and stratigraphy of the Ludlovian deposits of the Chelm borehole, Eastern Poland. *Studia geol. Pol.*, Warsaw, **13**: 1-88.
- 1969. The Silurian biostratigraphy of Poland based on graptolites. *Acta geol. pol.*, Warsaw, **19**: 393-501.
- TOGHILL, P. 1968a. The stratigraphical relationships of the earliest Monograptidae and the Dimorphograptidae. *Geol. Mag.*, London, **105**: 46-51.
- 1968b. The graptolite assemblages and zones of the Birkhill Shales (Lower Silurian) at Dobb's Linn. *Palaeontology*, London, **11**: 654-668.
- & STRACHAN, I. 1970. The graptolite fauna of Grieston Quarry, near Innerleithen, Peeblesshire. *Palaeontology*, London, **13**: 511-521.
- TÖRNQUIST, S. 1890. Undersökningar öfver Siljansområdets graptoliter. Pt I. *Acta Univ. lund.* **26**: 1-33.
- 1897. On the Diplograptidae and Heteroproniidae of the Scanian *Rastrites* beds. *Acta Univ. lund* **33** (5): 1-20, 2 pls.
- 1899. Researches into the Monograptidae of the Scanian *Rastrites* Beds. *Acta Univ. lund.* **35** (1): 1-25.
- URBANEK, A. 1958. Monograptidae from erratic boulders of Poland. *Palaeont. pol.*, Warsaw, **9**: 1-105.
- 1963. On generation and regeneration of cladia in some Upper Silurian monograptids. *Acta palaeont. pol.*, Warsaw, **8**: 135-254.
- 1966. On the morphology and evolution of the Cucullograptinae (Monograptidae, Graptolithina). *Acta palaeont. pol.*, Warsaw, **11**: 291-544.
- 1970. Neocucullograptinae n. subfam. (Graptolithina) - their evolution and stratigraphic bearing. *Acta palaeont. pol.*, Warsaw, **15**: 164-388.
- & RICKARDS, R. B. 1974. The ultrastructure of some retrolitids and graptoblasts. In RICKARDS, R. B., JACKSON, D. E. & HUGHES, C. P. (eds). Graptolite studies in honour of O. M. B. Bulman. *Spec. Pap. Palaeont.*, London, **13**: 177-186.
- WAERN, B. 1948. In WAERN, B., THORSLUND, P., HENNINGSMOEN, G. & SÄVE-SODERBERGH, G. Deep Boring through Ordovician and Silurian strata at Kinnekulle, Vestergötland. *Bull. geol. Instn Univ. Upsala* **32**: 337-474.
- WALKER, M. 1953. The sicula of *Monograptus scanicus* Tullberg. *Geol. Mag.*, London, **90**: 224-225.



- WARREN, P. T. 1971. The Sequence and Correlation of Graptolite Faunas from the Wenlock-Ludlow Rocks of North Wales. (Colloque ordovicien-silurien, Brest.) *Mém. Bur. Rech. géol. minier.*, Paris, **73**: 451-460.
- WOLFART, R., BENDER, F. & STEIN, V. 1968. Stratigraphie und Fauna des Ober-Ordoviziums (Caradoc-Ashgill) und Unter-Silurs (Unter-Llandovery) von Sudjordanien. *Geol. Jb.*, Hanover, **85**: 517-564.
- YANG D.-Q. 1964. Some Lower Silurian graptolites from Anji, Northwest Zhejiang (Chekiang). *Acta palaeont. sin.*, Peking, **12**: 629-636.
- YIN T. H. 1937. Brief description of the Ordovician and Silurian fossils from Shih-tien. *Bull. geol. Soc. China*, Peking, **16**: 281-302.

## X. INDEX

New taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (\*) denotes a figure.

- Abiesgraptus* 7\*, **82**, 95-6, 107  
*tenuiramosus* 83\*
- Agelograptus* *primus* 25  
*secundus* 25  
*zintchenkoae* 25
- Akidograptus* 7\*, 19, 24, 98-9  
*acuminatus* 26, 28, 30, 98  
*ascensus* **19-20**, 19\*, 28, 30, 88, **98-9**  
*precedens* 28  
*giganteus* 28, 99  
*priscus* 28  
*zhejiangensis* 28
- '*Amplexograptus*' 7\*, **11-13**, 97  
*innotatus* 13  
*inuiti* 13
- anagenesis 9-10
- Archiretiolites* 36
- Archiretiolitinae* 30
- Atavograptus* 5, 7\*, 41-3, 45, 86, 93, **102**, 103  
*atavus* 37\*, 38, **39-40**, 41, 43-4, 56-7, 64, 65\*, 102-3, 105; pl. 4, fig. 4; pl. 6, fig. 1  
group 5, 36, 39-41  
*ceryx* 37\*, 38\*, 38-41, 88, 102  
*gracilis* 39-40, 93, 102  
*praestrachani* 5, 37\*, 39-40, 54, **102-3**  
*renaudi* 39, 102  
*strachani* 7\*, 37\*, **39-40**, 42, 54, 102-3  
sp. 37\*, 39; pl. 4, fig. 5
- Atopograptus* 16
- Averianowograptus* 7\*, 73\*, 74\*, **74-6**, 106  
*magnificus* 74, 74\*
- Barrandeograptus* 7\*, 41, **72**, 95, 106  
*pulchellus* 72, 89, 95
- biserial graptoloids 19-36
- Bohemograptus* 7\*, 78, 81\*, **82**, 84, 96, 107  
*bohemicus* 81\*, 82  
*tenuis* 81\*
- cornutus* 81\*, 82  
*praecornutus* 81\*
- '*Bulmanograptus*' 7\*, 23, 25, 102  
*confertus* 28  
*decussatus* 28  
'bursts' of adaptive radiation 108
- '*Campograptus*' **52-4**, 73, 87  
*clingani* 48-9, 52, 53\*  
*communis* 7\*, 52-4, 53\*  
*obtusius* 52, 53\*  
*rostratus* 52, 53\*
- curtus* 52  
*elegans* 52  
*millipeda* 52-4, 53\*
- Cephalograptus* 7\*, **30**  
*acuminatus* 30  
*cometa* 30\*, 30, 88  
*extrema* 30\*, 30  
*tubulariformis* 30\*, 30
- cladia, sicular 95  
thecal 95-6
- cladogenetic divergence 9-10
- Climacograptus* 5, 7\*, 15, **16-19**, 17\*, 20-1, 24, 28, 33, 88, 97-8  
*alternis* 18\*, 19  
*hualross* 18  
*indivisus* 17\*, 18-19  
*innotatus* **11-13**, 12\*, 14, 90, 97  
*braziliensis* 11, 12\*  
*exquisitus* 11, 12\*  
*innotatus* 11, 12\*  
*jordaniensis* 11, 12\*, 97  
*nevadensis* 11  
*obesus* 11, 12\*  
*occidentalis* 11, 12\*, 13  
*pacificus* 11, 12\*, 13, **97**  
subsp. 11, 12\*
- inuiti* 13  
*latus* 18  
*manitoulinensis* 11, 12\*, 13



- medius* 17\*, 18; pl. 1, fig. 5  
*miserabilis* 17-19, 17\*  
*nebula* 16, 20, 98  
*normalis* 17-20, 17\*; pl. 2, fig. 3; pl. 3, fig. 4  
*premedius* 17\*, 18-19  
*rectangularis* 17\*, 18-19  
*scalaris* 17\*, 18  
*simplex* 98  
*supernus* 17  
*tamariscoides* 18\*, 20-1  
*toernquisti* 24  
*transgrediens* 7\*, 17\*, 18, 66, 107  
*typicalis* 12\*, 13, 97  
 sp. 17  
*Climoclimacograptus* 7\*, 14\*, 90  
   *retroversus* 14  
 'colonograptids' 7\*, 66  
   *admirabilis* 66  
   *bugensius* 66, 78-80  
   *chelmiensis* 66  
   *fecundus* 66  
   *graciosus* 66  
   *lochkovensis* 66  
   *perbrevis* 66  
   *samsonowiczi* 66  
   *transgrediens* see *Climacograptus*  
*Colonograptus* 67, 78, 107; see *Saetograptus*  
   *colonus* 7\*, 66, 77\*, 77-8  
 'Comograptus' *comatus* 21, 94, 99, 100, 100\*  
*Coremagraptus* 88  
*Coronograptus* 7\*, 40, 41, 42, 46, 86, 103  
   *cyphus* 7\*, 37\*, 41  
     *praematurus* 37\*, 41  
   group 36  
   *gregarius* 37\*, 41-2, 91-2, 103  
     *arcuatus* 41  
     *minisculus* 41  
   Zone 6, 98  
   *leei* 103  
   sp. Hutt 103; see *Monograptus*  
*Cucullograptus* 7\*, 82, 96; see *Lobograptus*  
   *aversus* *rostratus* 82, 84\*  
   *hemiaversus* 84\*  
   *pazdroi* 82, 84\*  
*cyrtograptids* 9, 106-7  
*Cyrtograptus* 7\*, 60, 73, 76-7, 92, 94-6  
   *canadensis* 75\*, 76  
   *centrifugus* 7\*, 74-6, 75\*  
   *coroniformis* 76  
   *ellesae* 75\*  
   *hamatus* 75\*, 77  
   *insectus* 7\*, 75\*, 76  
   *lapworthi* 7\*, 75\*, 76-7  
   *laqueus* 7\*, 75\*, 76  
   *lundgreni* 75\*  
   *mancki* 75\*, 77  
   *murchisoni* 34, 75\*, 76, 87  
     *bohemicus* 75  
   *parvulus* 76  
   *perneri* 75\*, 77  
   *radians* 75\*, 77  
   *ramosus* 75\*  
   *rigidus* 60, 75\*, 77  
     *cautleyensis* 75\*  
   *sakmaricus* 7\*, 75\*, 76  
   *shishkaticus* 76  
   *trilleri* 75  
*Cystograptus* 22\*, 23, 25, 90  
   *penna* 22\*, 25  
   *vesiculosus* 25; pl. 2, fig. 7  
  
*Damosiograptus* 74\*, 76, 106  
 'Demirastrites' 7\*, 46-7, 87  
   *denticulatus* 54  
   *sedgwickii* 7\*  
   *triangulatus* 46  
 'demirastritids' 37, 91, 107  
 dendroids 88  
 depositories of specimens 9  
*Dicellograptus* 94  
 didymograptids 94  
 dimorphograptids 8, 20, 86  
*Dimorphograptus* 7\*, 19, 23-4, 25, 86\*, 102;  
   see *Bulmanograptus*  
   *confertus* 28  
   *decussatus* 28, 91-2  
   *elongatus* 23, 24\*, 30, 86; pl. 1, fig. 3  
   *erectus* 86\*  
   *extenuatus* 24  
   sp. 23\*, 102  
*Diplograptus* 7\*, 8, 16, 20, 26, 28, 33  
   *africanus* 16  
   *diminutus* 16; pl. 1, fig. 6  
   *elongatus* 16  
   *fastigatus* 16  
   *fezzanensis* 16  
   *magnus* 16, 32\*, 33, 56; pl. 3, figs 1, 5;  
     pl. 4, figs 1-2  
   *modestus* 16; pl. 1, fig. 4  
     *applicatus* 16  
     *parvulus* 16  
     *tenuis* 16  
   ? *rarus* 16  
   *thuringiacus* 16  
 'Dittograptus' 100  
   *fortuitus* 101  
*Diversograptus* 7\*, 70\*, 71-2, 82, 95, 106  
   *capillaris* 70, 72

- ramosus* 70\*, 72  
*runcinatus* 69  
 dorsally curved rhabdosomes 86-7  
 evolutionary framework 9-11  
 Geological Society of America 9  
 'Globosograptus' 5, 7\*, 8, 57, 59, 61-2  
*Glyptograptus* 7\*, 15-16, 18\*, 20-1, 22\*, 23,  
 25-6, 38-9, 86, 94, 98-100; see  
*Pseudoglyptograptus*  
*avitus* 18\*, 20-1  
*cuneatus* 20  
 ? *curvithecatus* 25  
 ? *enodis* 26  
 ex gr. *fastigans* 20  
*nebula* 20, 98  
*nicholsoni* 20  
 aff. *nikolayevi* 20-1, 22\*, 26, 27\*  
*persculptus* 20-1, 22\*, 24-5, 38\*, 99, 99\*,  
 102; pl. 2, fig. 4  
*serratus barbatus* 21, 94-5, 99-100  
*sinuatus* 18\*, 20-2, 22\*, 24, 100  
*crateriformis* 20-1, 22\*  
*tamariscus* 18\*, 20-1  
*acutus* 21  
*linearis* 21  
*varians* 18\*, 19-21  
*tariti* 20  
 spp. 18\*, 20, 22\*, 38  
 gothograptids 8  
*Gothograptus* 7\*, 34-6, 35\*, 107  
*nassa* 34, 55  
 gracile rhabdosomes 92-3  
 Graptoloidea 97-106  
*Holoretiolites* 7\*, 8, 15, 34-6, 35\*, 90  
 Koren', Dr T. N. 8  
*Lagarograptus* 5-8, 7\*, 40-1, 42, 86, 90,  
 103-4  
*acinaces* 37\*, 42, 88, 90; pl. 6, fig. 3  
*inexpeditus* 37\*, 42, 104  
*tenuis* 37\*, 42, 90, 104  
 lineages 8  
*Linograptus* 7\*, 82-3, 95, 107  
*posthumus* 83\*  
*Lobograptus* 7\*, 82  
*cirrifer* 82, 84\*  
*expectatus* 82, 84  
*bicornis* 84\*  
*imitator* 82, 84\*  
*invertus* 84  
*progenitor* 82, 84\*  
*simplex* 82, 84\*  
*amphirostris* 84\*  
*parascanicus* 84\*  
*scanicus* 82, 84  
*'Mediograptus* 7\*, 59, 61, 62, 63\*, 93  
*kodymi* 63\*  
*kolihai* 63\*  
*minimus* 63\*  
*caulleyensis* 61, 61\*  
*Metaclimacograptus* 7\*, 14\*, 98  
*hughesi* 14-15; pl. 2, fig. 2  
*undulatus* 13-15, 15\*, 90, 97-8  
 sp. 98  
*Metadimorphograptus* 102  
*extenuatus* 24  
 monoclimacids 11, 37, 78, 106-8  
*Monoclimacis* 5, 7\*, 13, 20, 23, 40, 54-5, 57,  
 60, 62, 87, 89-90, 93  
*continens* 86  
*crenularis* 6, 7\*, 50\*, 54, 60  
*crenulata* 54; pl. 6, fig. 4  
*flumendosae* 11, 50\*, 55  
 ? *galaensis* 7\*, 50\*, 54, 60  
*griestoniensis* 50\*, 54, 55\*, 68\*, 71, 93  
*haupti* 55, 78; see *Pristiograptus*  
*micropoma* 55, 78-9  
*sublinnarssoni* 50  
*vomerina* 6, 50, 54, 55\*  
*vikensis* 50\*  
 ? sp. A 50\*, 54  
 spp. 50\*, 54  
 monograptids 8, 37, 86, 94, 108  
 origin of 36-9  
 monograptinid evolution 36-83  
*Monograptus* s.l. 15-16, 96-7  
*Monograptus* s.str. 5, 20, 23, 46, 55, 56-62,  
 69, 72-3, 78, 87, 89, 93-5, 104-7  
*aequabilis* 80  
*notoaequabilis* 80  
*angustidens* 80, 93  
*angustus* 93; see *Pribylograptus*  
*antennularius* 61, 63\*, 68  
*argenteus* 45, 51  
*cygneus* 51  
*austerus austerus* 37\*, 42-4, 43\*, 46-7, 91  
*bicornis* 37\*, 42-5, 43\*, 51, 91  
*praecursor* 42-5, 43\*, 51-2  
*sequens* 42-4, 43\*, 46, 52\*, 54  
*vulgaris* 42-5, 43\*  
 subsp. A 52  
*austerus* group 56, 58, 92

- balticus* 79-80, 93  
*barrandei* 63\*, 68  
*birchensis* 93  
*bouceki* 78  
*bugensis* 66, **78-80**  
*butovicensis* 88  
*capulus* 92  
*ceryx* 7\*, 23, 38; see *Atavograptus*  
*clingani* 48-9, 52, 53\*; pl. 4, fig. 3  
*colonus compactus* 62  
*communis* 44-5, 52, 58; see *Campograptus*  
 cf. *concinuus* 105  
*convolutus* 46-9, 47\*, 87; pl. 5, fig. 1  
*crispus* 59\*, 63\*  
*decipiens* 46, 47\*, 69\*  
*delicatulus* 47\*, 73, 73\*, 94, **104**  
*denticulatus* 46-9, 47\*, 52, 53\*  
*difformis* 42-4, 43\*, 46, 47\*, 92  
*discus* 87-8, 87\*; pl. 3, fig. 3  
*egregius* 88  
*elongatus* 104  
*exiguus* 68, 71-3, 72\*, 94; pl. 2, fig. 6  
*falcarius* 80  
*fimbriatus* 92  
*firmus* 50\*, 60  
*flemingii* 7\*, 50\*, 60-2, 93-4  
*flexilis* 50\*, 60, 107  
     *belophorus* 60  
*flexuosus* 63\*  
*formosus* 72\*, 78, 92, 107  
*fragilis fragilis* 64, 93; see *Pristiograptus*  
*gemmatus* 59\*  
*gracilis* see *Atavograptus*  
*gregarius* see *Coronograptus*  
*halli* 45, 49-51, 50\*, 60, 94  
*haupti* 55, 78-9; see *Pristiograptus*  
*helicoideus* 88  
*hemiodon* 80  
*hercynicus* 7\*, 62, **78-80**, 93, 107  
     *nevadensis* 93  
*incommodus* see *Pribylograptus*  
*involutus* 88  
*knockensis* 57\*, 58-9, 59\*, 63, 91, 93  
*leei* see *Coronograptus*  
*leintwardinensis* 78  
*limatulus* 44, 51  
*lobiferus* 7\*, 57\*, 58-60, 59\*, 62, 63\*, 69\*,  
     71-2, 92-3; pl. 5, fig. 4  
*ludensis* 7\*, 66\*, **77-8**, 77\*, 97  
*marri* 7\*, 48, 50\*, 54, 57, 60, 94; pl. 6,  
     fig. 2  
*microdon* 80, 87  
*millipeda* 52, 53\*, 58  
*minimus cautleyensis* 61  
*nodifer* 63\*, 67\*, 69, 94; see '*Streptograptus*  
     *tus*'  
*parapriodon* 50\*, 60, 93  
*perneri* 78  
*planus* 7\*, 45, 51, 76, 96  
*praehercynicus* 93  
*pragensis pragensis* 47  
     *ruzickai* 47  
*priodon* 7\*, 50\*, 54, 56-60, 93-4  
     line 10, 48-9, 55, 59-60, 62, 71, 94  
*proteus* 96, 96\*  
*pseudobecki* 63\*  
*pseudoplanus* 45, 51, 94, 96  
*radotinensis* 50, 60  
     *inclinatus* 50\*  
*ramstalensis* 78  
*rarus* see *Pristiograptus*  
*renaudi* see *Atavograptus*  
*retroflexus* 63\*  
*revolutus* 37\*, 42, 44-6, 104  
     *praecursor* 42, 52  
     subsp. A 52  
     subsp. C 104  
     groups **42-5**  
*riccartonensis* 50\*, 60  
*roemeri* 78; see *Pristiograptus*  
*runcinatus pertinax* 63\*  
     *runcinatus* 63\*, 69  
*sartorius* 63\*, 69\*  
*sedgwickii* 7\*, 45, **48-51**, 50\*, 56, 58, 60  
     69\*, 94; pl. 5, fig. 5  
*singularis* 57-9, 88, 91  
     *mancki* 59  
*spiralis* 46, 47\*, 72\*, 73, 75\*, 76, 78, 94;  
     see *Oktavites*  
*sudburiae* 7\*, 37\*, 41-5, **104**  
     group **45-6**, 89  
*telleri* 93  
*thomasi* 80  
*toernquisti* 5, 45, 51, 104  
     *elongatus* 104  
*triangulatus* 6, 46, 47\*, 92; pl. 5, fig. 3  
     *extremus* 46-7, 47\*  
     *fimbriatus* 46, 47\*; pl. 5, fig. 6  
     *major* 46\*, 47; pl. 5, fig. 2  
     *praedecipiens* 47-8  
     *separatus* 46, 47\*; pl. 2, fig. 2  
     *similis* 46, 47\*  
*tullbergi* 75\*, 76; see '*Spirograptus*'  
*turriculatus* 71\*, 72, 87-8, 94, **105**  
     *minor* 105  
*uncinatus* 7\*, 10, 62, 107  
 aff. *uncinatus orbatu*s 11  
*undulatus* 56-8, 57\*, 62, 69, 71-2, 93

- unguiferus* 62  
*uniformis* 78-80, 79\*, 93, 107  
*walkerae* 5, 43, 45, 51, 104  
*rheidolensis* 104  
*wimani* 63\*  
*yukonensis* 80, 107  
 sp. A 56-8, 56\*, 57\*, 61, 70, 93-4, 105  
 sp. B 57\*, 58, 61, 91, 93  
 sp. of Hutt 48, 58, 61, 68, 89\*, 91, 103  
 spp. 1 and 2 89, 91, 102; see *Atavograptus*  
 sp. 50\*, 57\*, 63\*, 70  
 monoserial graptoloids, origin 39  
 Montreal Congress 8-9
- Neocucullograptus* 81\*, 82  
*inexpectatus* 81\*  
*kozlowskii* 81\*  
*Neodiversograptus* 7\*, 82, 84, 95, 107  
*beklemishevi* 83\*  
*nilssoni* 82, 83\*  
*Neolobograptus* 7\*, 81\*, 82  
*auriculatus* 81\*, 82
- Obut, Professor A. M. 8, 73  
 'Oktavites' 62, 73, 106  
*exiguus* see *Monograptus*  
*spiralis* 7\*, 72\*, 73  
 Ordovician remnants 11-19  
*Orthograptus* 7\*, 15-16, 19, 23, 25-6, 27\*,  
 28-9, 33, 94, 100-1  
*acuminatus* 7\*, 26, 27\*, 28, 30, 88; pl. 2,  
 fig. 3  
*praematurus* 28  
*bellulus* 26, 27\*, 101  
*cyperoides* 26, 27\*, 101  
*eberleini* 26, 27\*  
*insectiformis* 26, 27\*, 101  
*malayornatus* 27\*  
*mutabilis* 26, 27\*, 29-30, 100-1  
*obuti* 26, 27\*, 101  
*quadrimumcronatus* 26  
*truncatus* 25, 86\*; pl. 1, fig. 7  
*abbreviatus* 26, 27\*  
 ? sp. 101
- Palaeontological Association 9  
*Paraclimacograptus* see *Climacograptus in-*  
*notatus*  
*Paraplectograptus* 7\*, 34, 35\*, 36  
 periderm entire, groups with 19-30  
 'Pernerograptus' 7\*, 43, 51; see *Monograptus*  
*austerus bicornis*, *praecursor* and  
*sequens*
- argenteus* 51  
*cygneus* 51  
*omulevkaensis* 51  
*sidjachenkoi* 51  
*Petalograptus* 7\*, 27\*, 28-9, 30\*, 33, 36  
*altissimus* 31, 34  
*elongatus* 28, 29\*  
*folium* 30, 30\*, 88  
*minor* 29; pl. 2, fig. 2  
*ovatoelongatus* 27\*, 29-30, 30\*  
*ovatus* 33  
*palmeus* 28, 29\*  
*wilsoni* 29  
 Plectograptinae 31, 107  
*Plectograptus* 7\*, 34, 35\*, 36, 107  
 ? *bouceki* 33-4  
 ? *textor* 34  
 ? sp. 35\*  
*Pribylograptus* 23, 39, 40-1, 44-5, 72, 86, 89,  
 103  
*angustus* 37\*, 41, 93  
*argutus* 7\*, 37\*, 40-1, 43, 45, 86  
*sequens* 41  
*incommodus* 37\*, 39-41, 45, 86, 103  
 group 36, 38  
 cf. *incommodus* 37\*, 40, 86, 89  
*jonesi* 41  
*leptotheca* 37\*, 40, 86, 88  
*sandersoni* 37\*, 40, 86  
 pristiograptids 37, 41, 66, 78, 82, 88, 107-8  
*Pristiograptus* 5, 7\*, 20, 41, 55, 62-7, 65\*,  
 75, 105-6  
*bugensis* 78, 93  
*chelmiensis* 93  
*concinus* 7\*, 64, 65\*  
*denemarkae* 67  
*dubius* 7\*, 62, 65-7, 66\*, 93  
*frequens* 66\*  
*latus* 67  
*ludlowensis* 67  
*fragilis fragilis* 64, 65\*, 93, 106\*  
 subsp. 64  
*frequens* 67  
*haupti* 55, 78-80  
*initialis* 7\*, 65\*, 67  
*jaculum* 64, 65\*  
*jaegeri* 66\*  
*kolednikensis* 66\*  
*kosoviensis* 80  
*largus* 65\*  
*lodenicensis* 66\*  
*ludensis* see *Monograptus*  
*meneghini* 7\*, 66\*, 67  
*nudus* 7\*, 64, 65\*, 67; pl. 2, fig. 5



- pergratus* 65\*, 67  
*praedubius* 7\*, 66–7  
*prantli* 65\*  
*pseudodubius* 7\*, 66\*, 67  
*pseudolatus* 67  
*rarus* 78, 79\*  
*regularis* 7\*, 64, 65\*, 67; pl. 5, fig. 7  
*roemeri* 78  
*transgrediens* 78, 80, 93  
*tumescens* 7\*, 66\*  
*variabilis* 64, 65\*  
*vicinus* 67  
*watneyae* 7\*, 64, 65\*  
 spp. 1 and 2 65\*, 105–6, 106\*  
 prothecal folds 94  
 protraction, proximal 88  
*Pseudoclimacograptus* 7\*, 13, 14–16, 14\*, 88, 98; see *Clinoclimacograptus*, *Metaclimacograptus*  
 cf. *clevensis* 14  
*orientalis* 14–15, 98  
*undulatus* see *Metaclimacograptus*  
*Pseudoglyptograptus* 7\*, 21–3, 22, 25, 90, 95; see 'Comograptus'  
*rhayaderensis* 21–3, 22\*, 100  
*tabukensis* 21–3, 22\*, 89, 100  
*vas* 21–3, 22\*  
 spp. 21, 23, 89  
*Pseudomonoclimacis* 55  
*Pseudoplegmatograptus* 7\*, 31, 33–4  
*altissimus* 32\*  
*obesus* 32\*  
*Pseudoretiolites* 7\*, 31, 33–4  
*dentatus* 33  
*perlatus* 32\*, 33  
*petalograptoides* 33  
*thuringicus* 33  
 sp. 33  
 ranges in time 6–8  
*Rastrites* 7\*, 46, 47–8, 87, 91–2  
*approximatus* 48, 49\*  
*geinitzi* 48, 49\*  
*carnicus* 48  
*distans* 48, 49\*  
*equidistans spengillensis* 92  
*fugax* 48, 49\*  
*hybridus* 48, 49\*  
*gracilis* 48, 49\*  
*linnaei* 48, 49\*  
*longispinus* 6, 46–9, 47\*  
*maximus* 48, 49\*, 60, 88  
*peregrinus* 46–8, 49\*  
*socialis* 47  
*perfectus* 48, 49\*  
*phleoides* 48, 49\*, 94  
*rastrum* 48, 49\*  
*richteri* 48, 49\*, 52–4, 53\*  
*spina* 48, 49\*, 57  
*rastritids* 37, 107  
 'Rectograptus' 26  
*truncatus* 26  
*Retiolites* 5, 7\*, 31–3, 34, 36, 88, 106  
*geinitzianus* 31–3, 32\*  
*angustidens* 31  
*retiolitids* 30–6, 94, 106  
*Retiolitinae* 31  
 retroversion 90  
 rhabdosome curvature, variable 86  
*Rhaphidograptus* 7\*, 22\*, 23, 24–5, 102  
*extenuatus* 24  
*maslovi* 25  
*toernquisti* 20–5, 22\*, 30, 88, 90, 99, 102;  
 pl. 1, figs 1, 2; pl. 2, fig. 1  
 ? *vicinus* 25  
 robust rhabdosomes 92–3  
*Saetograptus* 7\*, 77–8, 97, 107; see 'colono-graptids'  
*chimaera* 77–8  
*colonus* 7\*, 66, 77–8, 77\*  
*pilosus* 78  
*varians* 77–8, 77\*  
*willowensis* 78  
 Sennikov, N. 39  
 Silurian trends 83–96, 85\*  
*Sinodiversograptus* 7\*, 70\*, 71–2, 95  
*multibrachiatus* 70\*  
*Sinostomatograptus* 7\*, 31–3  
*occidentalis* 32\*  
 species abundance 8  
*Spinograptus* 7\*, 34–6, 35\*  
 spinosity, thecal and sicular 94–5  
 spiral rhabdosomes 86–7  
 'spirograptids' 78  
 'Spirograptus' 5, 7\*, 8, 72–3, 106  
*tullbergi* 7\*, 72, 75\*, 76  
*turriculatus* 72  
*Stomatograptus* 7\*, 31–3, 34, 106  
*grandis* 32\*  
 streptograptids 62, 63\*, 69  
 'Streptograptus' 7\*, 57, 59, 61–2, 63\*, 67–9, 71, 88, 106  
*antennularius* 61, 61\*, 68  
*exiguus* 68, 72\*  
*nodifer* 67–9, 67\*, 94  
 systematics 96–106

*Testograptus testis* 86-7  
 thecal asymmetry 96  
 thecal elongation 88  
 thecal hooks 90-1  
 thecal introversion 89  
 thecal isolation 91-2  
 thecal processes, ventral 90

thecal triangulation 92  
 trends 10, 83-96  
*Uralograptus* 7\*, 73\*, 74-6, 106  
     *insuetus* 74, 74\*  
 ventrally curved rhabdosomes 88  
 zones, standard scheme of 7\*, 9, 66

R. B. RICKARDS  
 SEDGWICK MUSEUM  
 CAMBRIDGE CB2 3EQ

J. E. HUTT  
 8 BINGHILL ROAD WEST  
 MILLTIMBER  
 ABERDEEN

W. B. N. BERRY  
*Dept of Paleontology*  
 UNIVERSITY OF CALIFORNIA  
 BERKELEY  
 CALIFORNIA  
 U.S.A.

Accepted for publication 26 February 1976



PLATE 1

***Rhaphidograptus toernquisti*** (Elles & Wood) (pp. 23, 102; see also Pl. 2, fig. 1)

FIG. 1. Q 5011. Skelgill Beds, *cyphus* Zone, Llandovery; Mealy Gill, Lake District.  $\times 10$ .

FIG. 2. Q 5012. As last.  $\times 10$ .

***Dimorphograptus elongatus*** Lapworth (p. 23)

FIG. 3. Q 5013. Skelgill Beds, *atavus* Zone, Llandovery; School Beck, Lake District.  $\times 5$ .

***Diplograptus modestus modestus*** Lapworth (p. 16)

FIG. 4. Q 5014. Skelgill Beds, Llandovery; Yewdale Beck, Lake District.  $\times 10$ .

***Climacograptus medius*** Törnquist (p. 18)

FIG. 5. Q 5015. *Acinaces* Zone, Llandovery; Clywedog Gorge, Montgomery, Powys, Wales.  
 $\times 10$ .

***Diplograptus* cf. *diminutus*** Elles & Wood (p. 16)

FIG. 6. Q 5016. *Persculptus* Zone, Llandovery; Yewdale Beck, Lake District.  $\times 10$ .

***Orthograptus truncatus*** Lapworth (p. 25)

FIG. 7. Q 5017. Hartfell Shales, Ordovician; Dobb's Linn, Moffat, Scotland.  $\times 10$ .





1



2



3



5



6



7



4

PLATE 2

***Rhaphidograptus toernquisti*** (Elles & Wood) (pp. 23, 102; see also Pl. 1, figs 1-2)

FIG. 1. Q 5018. Skelgill Beds, *atavus* Zone, Llandovery; Yewdale Beck, Lake District.  
× 10. Climacograptid aspect.

***Petalograptus* cf. *minor*** Elles (p. 29),

***Pseudoclimacograptus (Metaclimacograptus) hughesi*** (Nicholson) (p. 14) and  
***Monograptus triangulatus* cf. *separatus*** Sudbury (p. 46).

FIG. 2. Q 5019a-c. Skelgill Beds, *magnus* Zone, Llandovery; Skelgill, Lake District.  
× 10.

***Orthograptus acuminatus*** (Nicholson) (p. 28), and

fragments of ***Climacograptus normalis*** Lapworth (p. 17; see also Pl. 3, fig. 4)

FIG. 3. Q 5020a-b. Birkhill Shales, *acuminatus* Zone, Llandovery; Main Cliff, Dobb's  
Linn, Moffat, Scotland. × 5.

***Glyptograptus persculptus*** (Salter) (pp. 20, 99)

FIG. 4. Q 5021. *Persculptus* Zone, Llandovery; R. Severn, Montgomery, Powys, Wales.  
× 2½.

***Pristiograptus nudus*** (Lapworth) (p. 64)

FIG. 5. Q 5022. Browgill Beds, *crispus* Zone, Llandovery; Stockdale Beck, Lake District.  
× 10. On same slab as Fig. 6.

***Monograptus exiguus*** Nicholson (p. 73)

FIG. 6. Q 5023. × 10. Same locality and on same slab as Fig. 5.

***Cystograptus vesiculosus*** (Nicholson) (p. 25)

FIG. 7. Q 5024. Skelgill Beds, *atavus* Zone, Llandovery; Yewdale Beck, Lake District.  
× 10. Sicula and first few thecae.





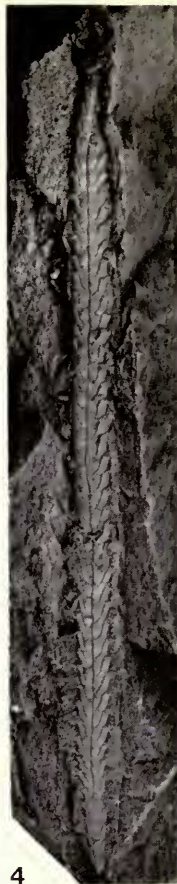
1



2



3



4



5



6



7

PLATE 3

***Diplograptus magnus*** H. Lapworth (p. 16)

FIG. 1. Q 5025. *Magnus* Zone, Llandovery ; Clywedog Gorge, Montgomery, Powys, Wales.  $\times 10$ .

FIG. 5. Q 5029. *Magnus* Zone, Llandovery ; stream south of Blackman's Hall, Van Mines, Montgomery, Powys, Wales.  $\times 10$ . Specimens showing varied preservation and deformation.

***Petalograptus*** sp. (p. 29)

FIG. 2. Q 5026. *Cometa* horizon, *convolutus* Zone, Llandovery ; Dobb's Linn, Moffat, Scotland.  $\times 10$ .

***Monograptus discus*** Törnquist (p. 87)

FIG. 3. Q 5027. Skelgill Beds, *crispus* Zone, Llandovery ; Stockdale Beck, Lake District.  $\times 10$ .

***Climacograptus normalis*** Lapworth (p. 17 ; see also Pl. 2, fig. 3)

FIG. 4. Q 5028. Skelgill Beds, *acuminatus* Zone, Llandovery ; Yewdale Beck, Lake District.  $\times 10$ . Specimen deformed, lineation at right angles to length of rhabdosome.



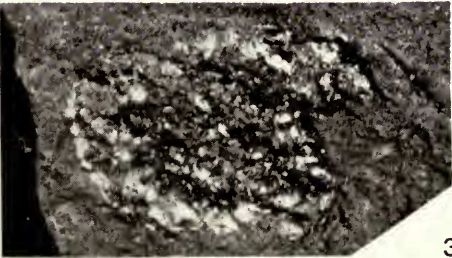
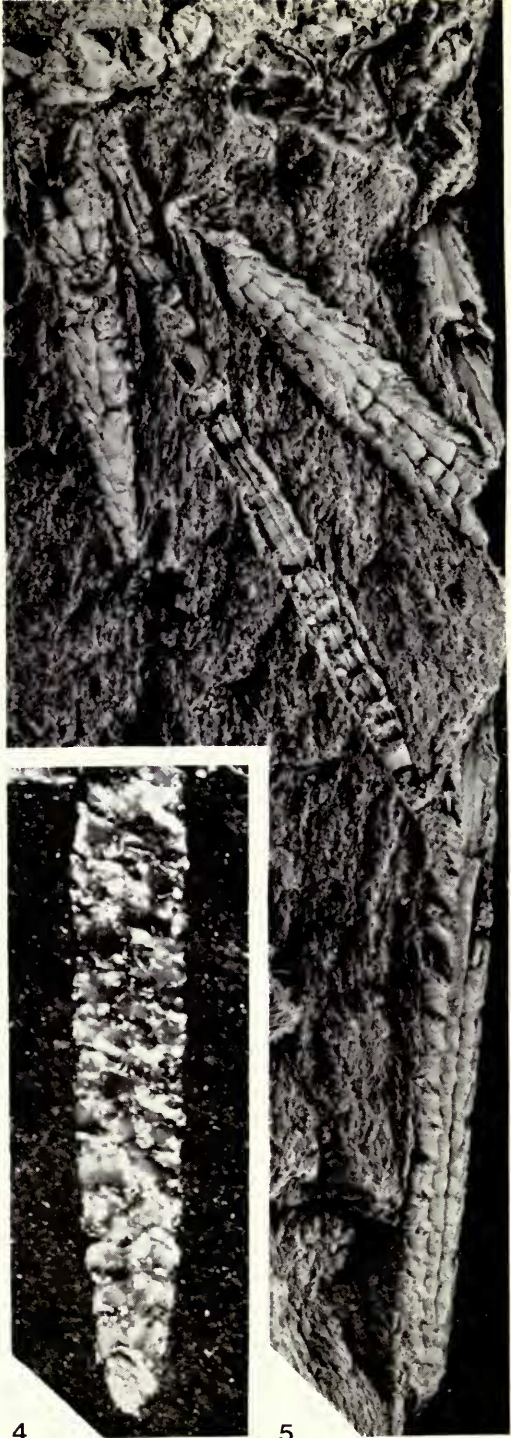
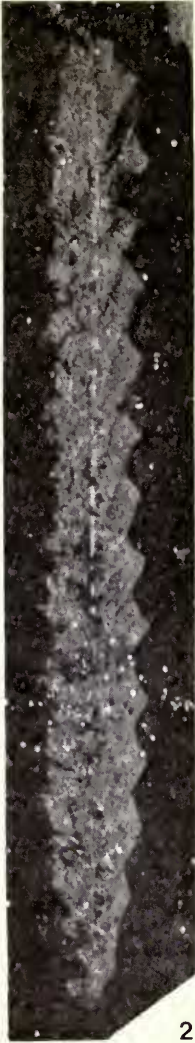


PLATE 4

cf. *Diplograptus magnus* H. Lapworth (p. 16)

FIG. 1. Q 5030. *Magnus* Zone, Llandovery ; stream south of Blackman's Hall, Van Mines, Montgomery, Powys, Wales.  $\times 10$ . Reverse view.

FIG. 2. Q 5031. As last.  $\times 10$ .

*Monograptus clingani* (Carruthers) (p. 52)

FIG. 3. Q 5032. Birkhill Shales, Llandovery ; Dobb's Linn, Moffat, Scotland.  $\times 10$ .

*Atavograptus atavus* (Jones) (pp. 38-40 ; see also Pl. 6, fig. 1)

FIG. 4. Q 5033. Skelgill Beds, *cyphus* Zone, Llandovery ; Mealy Gill, Lake District.  $\times 5$ .

*Atavograptus* sp. [= *Monograptus* sp. 2 of Hutt & Rickards 1970 : 76] (p. 39)

FIG. 5. Q 5034. Skelgill Beds, *atavus* Zone, Llandovery ; School Beck, Lake District.  $\times 1$ . Hundreds of current-sorted rhabdosomes ; at the top of the illustration the actual thickness of piled and flattened rhabdosomes is 3 mm.





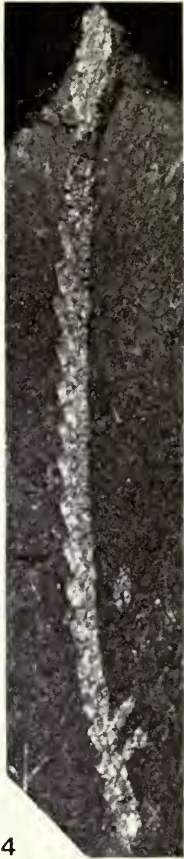
1



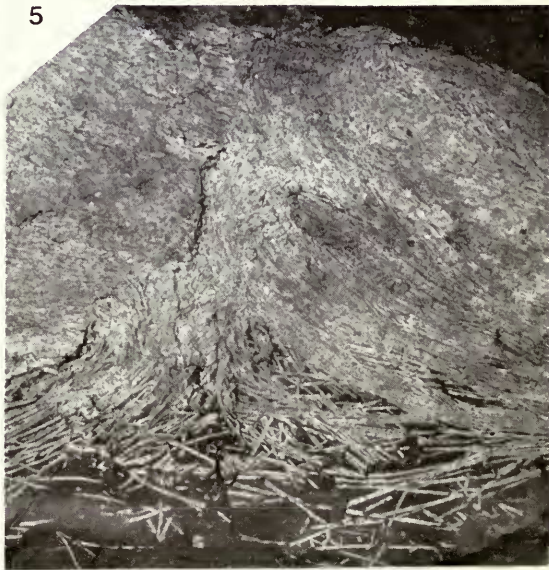
2



3



4



5

PLATE 5

***Monograptus convolutus*** (Hisinger) (p. 46)

FIG. 1. Q 5035. *Cometa* horizon, *convolutus* Zone, Llandovery ; Clywedog Gorge, Montgomery, Powys, Wales.  $\times 10$ .

***Monograptus triangulatus*** cf. *major* Elles & Wood (p. 46)

FIG. 2. Q 5036. *Leptotheca* Zone, Llandovery ; south-east of Pwll-gwinau, Nant yr Hebog, Montgomery, Powys, Wales.  $\times 5$ .

***Monograptus triangulatus triangulatus*** (Harkness) (p. 46)

FIG. 3. Q 5037. '*Gregarius*' Zone, Llandovery ; Dobb's Linn, Moffat, Scotland.  $\times 10$ .

***Monograptus lobiferus*** M'Coy (p. 58)

FIG. 4. Q 5038. *Convolutus* Zone, Llandovery ; Bron Felin, near Old Hall, R. Severn, Montgomery, Powys, Wales.  $\times 5$ .

***Monograptus sedgwickii*** (Portlock) (p. 48)

FIG. 5. Q 5039. *Sedgwickii* Zone, Llandovery ; Church Beck, Lake District.  $\times 5$ .

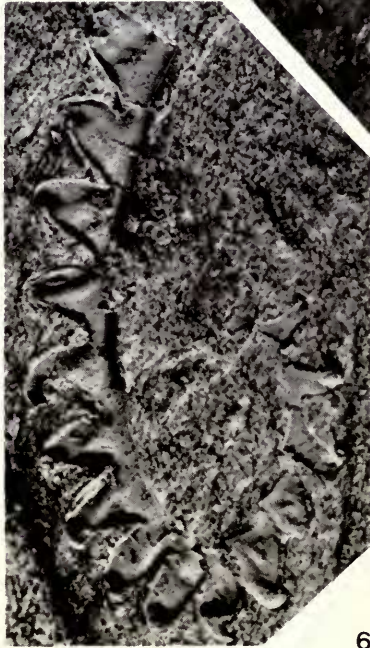
***Monograptus triangulatus fimbriatus*** (Nicholson) (p. 46)

FIG. 6. Q 5040. Skelgill Beds, *magnus* Zone, Llandovery ; Skelgill, Lake District.  $\times 10$ .

***Pristiograptus regularis*** Törnquist (p. 64)

FIG. 7. Q 5041. *Convolutus* Zone, Llandovery ; Bron Felin, near Old Hall, R. Severn, Montgomery, Powys, Wales.  $\times 5$ .





1

2

3

4

5

6

7

PLATE 6

***Atavograptus atavus*** (Jones) (pp. 38-40 ; see also Pl. 4, fig. 4)

FIG. 1. Q 5042. Skelgill Beds, *cyphus* Zone, Llandovery ; Yewdale Beck, Lake District.  
× 5. Distal thecae in relief.

***Monograptus marri*** (Perner) (pp. 48, 60)

FIG. 2. Q 5043. Browgill Beds, *crispus* Zone, Llandovery ; Stockdale Beck, Lake District.  
× 10. Distal thecae, lineation showing direction of elongation at right angles to rhabdosome length.

***Lagarograptus acinaces*** (Törnquist) (p. 42)

FIG. 3. Q 5044. *Acinaces* Zone, Llandovery ; Blackman's Hall, Van Mines, Montgomery, Powys, Wales. × 5. Specimen lacking preserved ventral apertural processes.

***Monoclimacis crenulata*** *sensu* Elles & Wood (p. 54)

FIG. 4. Q 5045. *Crenulata* Zone, Llandovery ; Tach Wood, Glyn Brook, Montgomery, Powys, Wales. × 5. Showing thecal eversion and thecal processes.



